Vol. XII, Part 2 May, 1960

THE
QUARTERLY JOURNAL
OF
EXPERIMENTAL PSYCHOLOGY

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PUBLISHED FOR
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BY
W. HEFFER & SONS LTD. CAMBRIDGE

OCCUPATIONAL PSYCHOLOGY

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April, 1960 VOLUME 34, No. 2

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THE QUARTERLY JOURNAL OF
EXPERIMENTAL PSYCHOLOGY

Vol. XII 1960 Part 2

PERCEPTUAL CAPACITY OF THE ISOLATED VISUAL CORTEX IN THE CAT

BY

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The split-brain approach was utilized in 6 cats to test the degree of functional autonomy in the visual system. The central visual cortex of one hemisphere was isolated by the removal of most of the extravisual neocortex of the same hemisphere. Visual inflow was restricted to the isolated side in four cases by sectioning the crossed optic fibres at the chiasma and masking one eye and in two cases by section of the contralateral optic tract. The isolation produced severe deficits in visual performance, although all cases retained some ability to learn and to recall simple pattern discriminations. The results of two- and three-stage removals of the non-visual cortex, and of terminal section of the callosum, as well as histology of the lateral geniculate nucleus indicated that geniculo-striate damage was not the limiting factor. Removal of fronto-parietal cortex produced as much or more decrement in visual discrimination than did removal of temporal cortex.

INTRODUCTION

It has been found that the somatic cortex is capable of mediating high level perceptual learning and memory in the cat after its isolation by removal of parietal, occipital, and temporal cortex and section of the corpus callosum (Sperry, 1959). The aim of the following was to find out to what extent visual functions might survive similar isolation of the optic cortex. Visual impairments produced by bilateral removal of the frontal eye fields (Fulton, 1955) or the infero-temporal cortex (Chow and Orbach, 1957) suggest the probability of less functional independence in this system. On the other hand, Lashley's findings (1942, 1950) as well as the fibre relations of the striate cortex point to the possibility of a degree of functional autonomy.

The present study involved isolation of the visual cortex of only one hemisphere, the corpus callosum being sectioned and the visual inflow restricted to the same hemisphere. Earlier work has shown that cats and monkeys with midline section of the chiasma and callosum are unable to perform with one eye visual discriminations learned through the other eye (Downer, 1958, 1959; Myers, 1955, 1956; Sperry, 1958; Sperry, Stamm and Miner, 1956). This makes it possible to study the perceptual and mnemonic functions of the isolated visual cortex unilaterally, confining the extensive cortical removals to one side while the other hemisphere is kept intact to prevent paralysis and to serve general background function.

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METHOD

Restriction of the visual inflow to one side was effected in four cases by sectioning the optic chiasma and masking one eye during training and testing following techniques developed earlier by Myers (1955). In two other cases (*Chr*, *Ltm*) it was effected by section of the left optic tract just posterior to the chiasma. The animals were adult cats selected as they became available after serving in other experiments.

The operated animals with vision restricted were taught to perform one of several simple pattern discriminations (see Fig. 1) which were stabilized by overtraining a minimum of 400 trials. Isolation of the central cortical area for vision was then carried out by removal of the surrounding neocortex in one or more stages and by transection of the corpus callosum, the order of the surgical steps being varied in the different cases as described below. Standard surgical precedures were followed throughout. Callosal section was effected by exposure and retraction of the hemisphere opposite the visual area to be tested to avoid damage to the latter. Special effort was made to preserve the larger branches of the middle cerebral artery running to the lateral edge of the isolated cortex.

Training and testing of visual discriminations was carried out by procedures described elsewhere (Sperry, Miner, and Myers, 1955). In brief, the cats were placed in a darkened training box (see Fig. 2) at one end of which were two swinging windows or doors each containing a transilluminated test figure. The test patterns were interchanged from right to left at random and the animals learned to push open the door holding the correct (rewarded) figure. Correct choices were rewarded with morsels of food; incorrect choices were signalled by a buzzer. Tests of generalized visual function were also applied, including visual placing responses, centring and following reactions, avoiding objects in walking, and others as described below.

The brains, following fixation and removal, were checked by gross and microscopic examination. The test hemisphere including the lateral geniculate nuclei was sectioned at 25 μ and stained with cresyl violet. The text figures indicating the cortical removals on a type feline hemisphere are based on examination of the removed brains and on maps drawn at the time of operation. On the medial surface the lesions were continued directly downward to the corpus callosum anteriorly and to the splenial fissure and pyriform lobe posteriorly.

OBSERVATIONS

Removal of non-visual cortex in one stage. In the first case, *Wzl*, the cortical removal was carried out in one stage to the extent indicated in Figure 3. The lateral extension into the auditory region was left intact in this and later cases to avoid damage to the underlying optic radiations. To casual examination the animal appeared to be blind on the affected (left) side during the first two weeks after the cortical removal. It seemed unable to see pieces of food held directly in front of it; it would not jump to the floor from a stool 40 cm. high; and it bumped into objects in walking about a room. Forced circling to the left was pronounced in the first two weeks, more so than in any of the subsequent cases. The tendency to veer to the left had almost disappeared at the end of five weeks. During these first five weeks discriminative performance through the left eye in the testing apparatus failed to rise above chance.

Two months after the cortical removal, *Wzl* had regained the ability to discriminate the light vs. dark patterns L–D. It then relearned discriminations H–V and X–O with no evidence of any retention from the preoperative training. The performance on X–O was erratic, but on H–V *Wzl* attained a consistent performance level of 92 per cent. correct responses.

Section of the corpus callosum four months after the cortical removal again abolished all discriminations up to five weeks after the operation. Beginning with the sixth week after callosal section, discriminations L–D and H–V were relearned a little easier than initially, suggesting some saving. *Wzl* learned further to discriminate a horizontal bar from an upright bar that was tilted from the vertical by stages up to 30°. Beyond this angle the discrimination broke down.

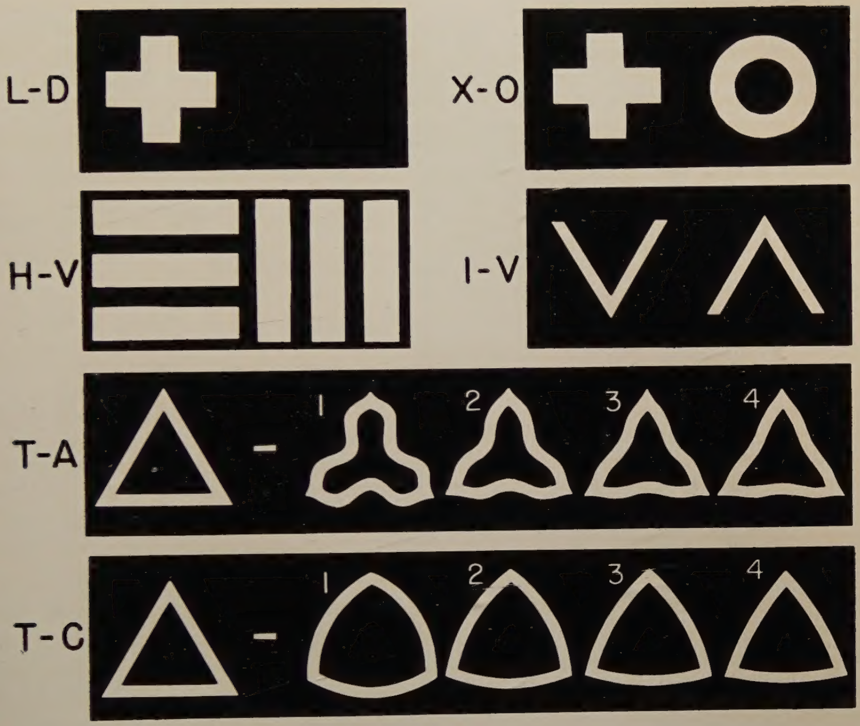

FIGURE I

Pairs of patterns used in testing visual discrimination. In T–A and T–C only one of the distorted triangle series was paired with the equilateral triangle at left.

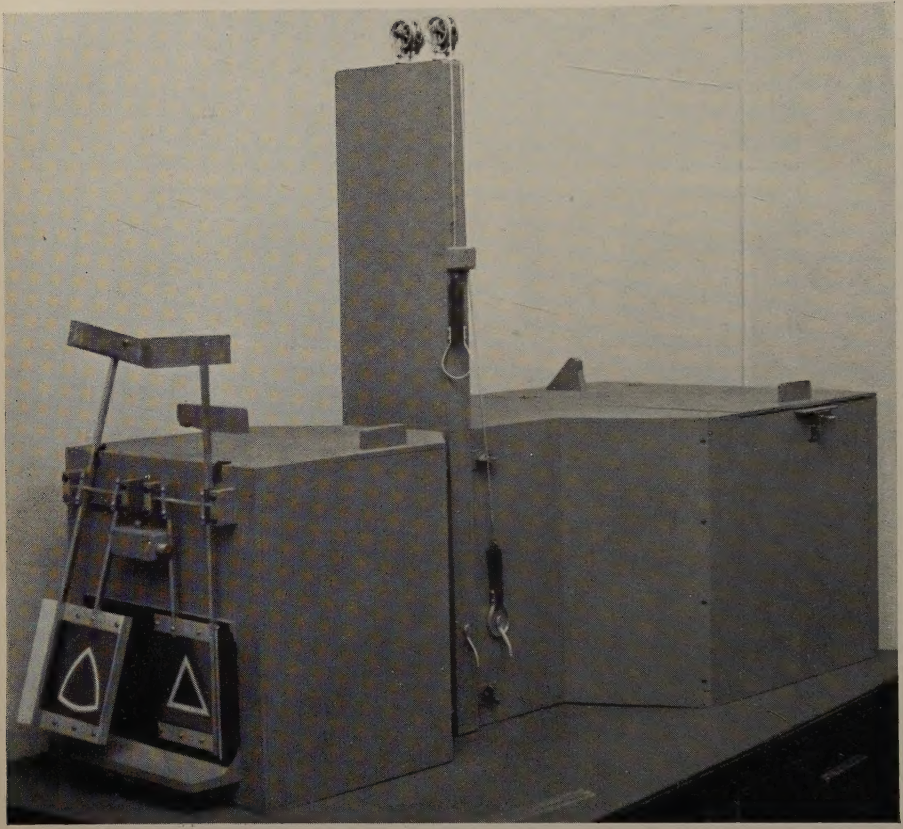

FIGURE 2

Discrimination apparatus. Starting chamber is separated from choice chamber by two sliding doors, one opaque, one transparent.

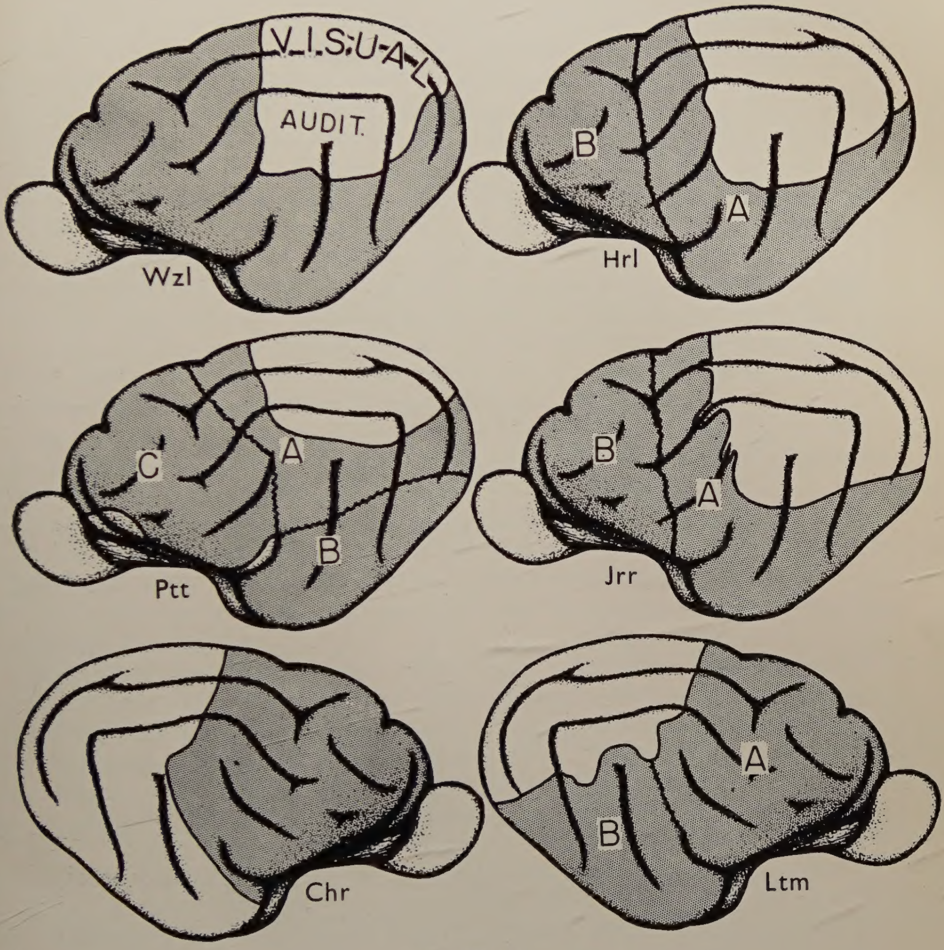

FIGURE 3

Extent of cortical removals (stippled) in test hemisphere. Where the removals were carried out in stages, the order is indicated alphabetically.

In further visual tests with the left eye conducted at three months after section of the callosum we were unable to evoke centring, fixating, or following movements of head and eyes. In walking about an unfamiliar room, the animal bumped into objects directly centred in its path. Visual placing responses were absent as were also the reaching for and striking at small objects. The animal would not jump from one table to another of equal height at 25 cm. distant and balked at jumping to the floor from a low stool. The cat seemed unable to see pieces of meat dangled close in front of its nose. In the discrimination apparatus its performance was very slow and uncertain, and it seemed to tire easily. It would typically run a good series of 9 to 15 perfect runs, then relapse with many errors.

Removal of non-visual cortex in two stages. In the next case, *Hrl*, a wide band of the left cortex bordering the area to be isolated (A in Fig. 3) was removed first so that any damage to the underlying fibre systems would be limited mostly, or entirely to this first stage operation. The preoperatively trained H–V survived this removal with only a transient drop in performance level that was recovered by the 14th day after operation.

On the 18th day following the cortical removal, the corpus callosum was sectioned. During the next ten days the animal appeared blind in the left eye. By the 20th day it was again able to discriminate H–V, and was performing 98 to 100 per cent. correct during the three weeks preceding the final cortical removal. Its visual performance in general remained relatively good.

The remaining frontal region of the left cortex was removed four months after the callosum had been sectioned. This produced an additional impairment of vision, evident both in general tests and in the discrimination box. Beginning 43 days after this operation *Hrl* was again able to discriminate H–V, and like *Wzl*, it learned to distinguish a horizontal bar from one tilted up to 30° from vertical. Other tests of general visual function administered during the 12th week after the final operation yielded much the same results as obtained in the final stage in the preceding case.

Removal of non-visual cortex in three stages. The third case, *Ptt*, was trained to discriminate H–V, X–O, and I–V following transection of the optic chiasm, and the callosal and hippocampal commissures. The first cortical removal involved the area A shown in Figure 3. Discrimination H–V survived with moderately good performance, but X–O and I–V had to be relearned. However, the relearning went rapidly, suggesting partial retention, particularly for X–O.

After consistent performance had been restored on all three discriminations, cortical area B (Fig. 3) was removed 32 days after the removal of A. Discrimination H–V and X–O survived this second removal, but I–V was lost. With retraining, the performance levelled off on H–V at 88 per cent., and on X–O at only 68 per cent. correct.

When the isolation was completed by removal of the frontal region 43 days after removal of B, the effect was much the same as the final stage in the two preceding cases. In the course of six weeks it was possible to retrain H–V and X–O, but not I–V on which there was no sign of improvement after 750 trials. In this final condition *Ptt*, like *Wzl* and *Hrl*, failed to respond visually to food dangled in front of its nose; it walked directly into objects; and in general exhibited much the same picture of visual deficiency as had cases *Wzl* and *Hrl*.

Less drastic removal, two stages. In this fourth case, *Jrr*, the cortical removals were much like those in *Hrl* except that a larger cortical area was left intact (Fig. 3). Particularly the depths of the anterior ectosylvian and suprasylvian fissures were intentionally preserved to avoid damage to possibly important fibres coursing from the intact cortical area forward into the internal capsule and basal ganglia. In this case the callosum and anterior and hippocampal commissures, as well as the optic chiasm had previously been sectioned and the cat had been trained to perform all the discriminations shown in Figure 1.

The first step in cortical removal involved the area A shown in Figure 3. All the discriminations survived this except I–V, which was quickly restored to the criterion level of 17 out of 20 correct by the 60th trial. Discriminations I–V and T–A3 levelled off at 85 per cent. correct, the others above 90 per cent.

Two months after the removal of A, the remaining frontal neocortex was removed on the same side. Discriminations H–V and X–O were both retained although the performance was much more erratic than before the operation. T–C1 was retained and it was possible to retrain T–C2 but not T–C3. T–A3 was lost but it was possible to retrain T–A2. The performance levelled off between 79 per cent. correct on T–C2 up to 84 per cent. for H–V. The I–V discrimination was lost and could not be retrained.

In the general visual tests this case was somewhat superior to the others. It could centre its gaze on a piece of meat approximately 3 cm. in length held 20 cm. away and could follow the movement of small objects across the middle of the visual field. Visual placing reactions with the left foot were present, though they usually fell short. Unlike the others, this cat seldom bumped into objects in walking an unfamiliar room except when they were approached from the blind half of the visual field.

Visual area isolation with tract section. The experiments were repeated in two additional cases in which the visual inflow was lateralized by section of the left optic tract just posterior to the chiasma. Tract section has the advantage of leaving the crossed as well as the uncrossed optic inflow to the test hemisphere. It also obviates masking one eye during training and testing. In general the visual impairment under these conditions was of much the same order as in the preceding with the following worth special mention.

In both cases the frontal area, labelled A in *Ltm* in Figure 3, was removed first. This produced an impairment as great as or more severe than when the temporal and parietal removals were first. By the third month after this removal the discriminations H–V, X–O, and T–A1 had been recovered to a level of 90 per cent. or better.

The temporal area (B in Fig. 3) was removed in *Ltm* six months after the frontal removal. Beginning eight weeks later *Ltm* again began to perform H–V and X–O and attained levels of 95 and 90 per cent. correct, respectively, by the tenth and eleventh weeks. When the callosum was sectioned in *Ltm* six months after the temporal removal, discrimination was reduced to a level of pure chance for three weeks. Beginning on the 4th week, H–V came back and reached a level of 84 per cent. correct. Three months later *Ltm* was still unable to perform X–O and in the general tests also it displayed a degree of visual defect much like the final stage in *Wzl, Hrl* and *Ptt.*

In *Chr* section of the callosum five months after the frontal removal abolished pattern discrimination for three weeks, after which X–O and T–A1 were recovered. However, the performance of these did not rise above 80 per cent. correct during the next three months. The animal continued to perform so slowly and poorly that the temporal removal was not carried out.

Weak centering and following reactions, as well as visual placing, survived in both *Chr* and *Ltm*. Curiously, the callosal section in *Chr* left a pronounced asymmetry in pupillary size, the right pupil being dilated. This was still present, though less marked, as much as a year later. The pupillary effect was absent or at least much less striking in *Ltm*. All the chiasma-sectioned cases exhibited the lasting bilateral dilation that typically follows chiasma section in the cat.

When the discrimination tests were completed, *Ltm* and *Chr* were used further in a conditioned reflex study (Voneida and Sperry, unpublished). With a flashing light serving as the signal stimulus which was paired with an electric shock to the right paw, it was possible to establish in both cases a conditioned lifting of the right paw to the visual signal.

Anatomical Checks

Examination of the removed brains showed the following: Section of the crossed fibres in the chiasma was complete in *Wzl*, *Hrl*, *Ptt*, and *Jrr*. The left optic tract was also completely sectioned in *Chr* and *Ltm*. Division of the corpus callosum and adjacent psalterium was complete with the following two exceptions: A fine strand of fibres no more than 1·0 mm. in diameter was intact at the posterior edge of the callosum in *Ptt*. The anterior fourth of the callosum was intact in *Hrl*, but it was hardened and presumably degenerate owing to removal of all its cortical connections on the left side.

Examination of right and left lateral geniculate bodies in the chiasma-sectioned cases revealed patches of retrograde degeneration on the isolated side. These degenerate areas were located on the edges, however, and in the cases most severely affected, *Wzl* and *Hrl*, the degenerate areas did not total more than half the volume of the principal dorsal nucleus. Extensive retrograde changes were apparent in the thalamus on the isolated side. The hippocampus, and amygdaloid nuclei were undamaged for the most part as was also the pyriform lobe except for minor invasion of the lateral pyriform area in three cases. On the medial surface most of gyrus proreus was intact in *Jrr*. Smaller remnants of the cingulate and proreus gyri were found on the medial surface in other cases, but no correlation between these and the experimental results was evident.

Discussion

The experiment was undertaken initially on the assumption that directionality in vision is perceived with reference to body posture, especially that of the head and eyes, and hence if all somesthetic cues for posture could be prevented from integrating with the retinal cues, it should have profound effects on visual function. Although the results are in line with this reasoning, they are by no means conclusive.

Removal of the temporal cortex produced no greater, and perhaps somewhat less impairment of vision than did removal of the frontal region. It would appear that the inferotemporal cortex does not play the critical rôle for visual perception in the cat that it does in the monkey (Chow and Orbach, 1957). The nature of the extravisual contribution is quite unknown. The cats acted as if the impairment involved the perceptual process itself rather than its motor expression.

It should be emphasized that survival of the training-box discrimination of the simpler patterns employed in this study is indicative of only a very low level of perception. Even with the entire visual cortex removed bilaterally, the cat may still respond to differences in light intensity and to moving vertical stripes (Smith, Kappauf, and Bojar, 1940). Thus, by using head or eye movements, the cats could conceivably have performed L–D, H–V, and X–O with little use of the isolated area. Actually, head movement did not appear to be used to facilitate the discrimination in this way. Eye movements were not observable.

The visual impairments were not simply a reflection of geniculostriate damage judging from the histology of the lateral geniculate body. The fact that additional impairments were produced by the removal of the distant frontal and temporal lobes after the cortex between these and the preserved occipital remnant had already been removed at an earlier date, gave further indication that the deficits were not attributable to damage either to underlying projection fibres or to circulatory or other secondary damage within the isolated cortex.

The visual deficits were least severe in *Jrr*. The intact cortex that set off this case from the others seemed to be primarily the depths of the anterior ectosylvian and anterior sylvian fissures. This points to the possibility that the cortex here or the fibre systems underlying it have special importance for vision. However, much more analysis will be needed to determine the relative importance of the various cortical areas involved. In general the results point to the probability of several or multiple extravisual factors with a "mass action" type of effect.

In a related experiment in progress somewhat similar isolation of the occipital cortex in a split-brain monkey with sparing of the geniculostriate tract has been observed (Sperry, unpublished) to produce even a greater blinding effect than in the cat.

The transient blindness of one to several weeks' duration produced on the isolated side by section of the corpus callosum was in part presumably a manifestation of diaschisis potentiated by the preceding cortical removals. Diaschisis from major neocortical damage seems in our experience not to be fully recovered before about six to eight weeks in the cat. This fits with the observed period for recovery and enhancement of evoked cortical potentials in areas affected by callosal degeneration (Franklin and Desmedt, 1957). Some of the added impairment produced by callosal section persisted well beyond this period in *Ltm* and *Chr*. This would suggest that sensory or perceptual data were being communicated over the callosum for efferent processing by the more efficient, intact hemisphere.

The visual placing response survived isolation of the visual cortex and the paw preferred was the one contralateral to the remaining somatic area despite the surgical separation of the latter from the receiving visual cortex. This fits with the observation (Schrier and Sperry, 1959) that the split-brain cat can use either paw with equal correctness in learning and performing monocular discriminations.

The work was supported by the F. P. Hixon Fund of the California Institute of Technology and by research grants from the National Science Foundation and the Southern California Society for Mental Hygiene. The valuable assistance of Lois MacBird and Alice McCulloch in the training and testing is gratefully acknowledged.

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GROUPING OF STIMULI AND APPARENT EXCEPTIONS TO THE PSYCHOLOGICAL REFRACTORY PERIOD

BY

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When a subject is called upon to respond independently to two stimuli, the second of the two responses is often delayed if the stimuli follow closely on one another, and this has led to the suggestion that in making decisions the human operator accepts and organizes the available input information intermittently in the manner of a discontinuous servo. According to this view two nearly simultaneous stimuli can only be dealt with equally fast if they are grouped into a single decision to respond to both stimuli; otherwise one will have to wait for the attention of the central mechanism until the other has been dealt with. In the present experiment it is shown that delays in the second response are not necessary or invariable, and that the pattern and timing of the second responses when they are performed without delay differ in important respects from those to be expected of grouped responses. It is concluded that the central mechanisms concerned in the response do not possess the limitations that the single channel theory would suggest.

Introduction

It is widely held that one cannot attend to more than one thing at once, but this statement is vague in that it does not make clear what is meant by "one thing." Even simple sensations involve a complex input from many sensory receptors. However, it has been suggested (e.g. Hick and Welford, 1956) that at least the "decision process," intervening between the central arrival of a sensory stimulus and the central initiation of a response, is a process which takes place in, and has to be routed through, a single central channel, and that this mechanism acts in an intermittent manner, dealing with only one set of data during the finite time it takes to reach its decision and initiate the appropriate response. Input information is gated into the central channel intermittently and is allowed in only *before* the commencement of the period ("central organizing time") during which it is translated into an appropriate output; information arriving later cannot be used to influence the response, but must be discarded or held in store until the channel is cleared. Similarly, information relative to a decision about some other response will also have to wait until the first response is organized and initiated; only then can the organization of the second response begin. Thus even if the two responses involve quite independent sensory and motor pathways, the second will be delayed if it arrives centrally while the first is still engaging the hypothetical single central channel.

This model was evolved by a number of earlier workers (Craik, 1947, 1948; Vince, 1948; Hick, 1948) to explain the experimental data on which the concept of the "psychological refractory period" is based. Welford (1952) gave the theory a quantitative form, and considered in detail the possible further hypotheses and refinements that were needed to enable it to allow for the experimental data then available. Davis (1956, 1957) rejects some of the details of Welford's model, but accepts the main concepts outlined above and has provided some further experimental support.

In Welford's model, the lengthening of the second response, which occurs if the appropriate stimulus arrives before the hypothetical "decision process" to the first is over, depends quite simply on the difference between the interstimulus interval (I) and the length of the first reaction time (RT_1), so that the actual $RT_2 = RT_N + RT_1 - I$, where RT_N is what RT_2 would have been were there no interfering first stimulus. When plotted this relationship will be represented by a straight line with a negative slope of 45°, falling from a maximum when the second stimulus (S_2) occurs at the earliest distinguishable interval after the first. It may be added that if, rather than taking RT_1 itself, one reduces this value to allow for motor conduction time, the slope of the predicted RT_2 remains the same, though its height and length would be altered by the corresponding amount.

Not all the experimental results have fitted this prediction. Elithorn and Lawrence (1955) showed that in one situation the longest second reaction times might occur when the second stimulus came, not immediately, but 50 to 250 millisec. after the first. Moreover, in their subjects this slowing of the early second responses tended to be selectively "learnt out" during the course of the experiment.

But this is not decisive evidence against the intermittency hypothesis. Welford, in his original paper (1952), had already considered certain apparent exceptions to the "psychological refractory period" noticed by Vince (1948); he concluded, with her, that they were not true exceptions at all, but examples of "grouping," the two stimuli being responded to, not separately and consecutively, but as a single situation, i.e. "together." It is suggested that in certain circumstances this can occur when the two stimuli are separated by an interval of anything up to 50 to 100 millisec., and that it is associated with conscious or unconscious waiting for a brief period, during which the subject decides whether a second stimulus is coming almost at once.

There appear to be several possible criteria which can be adopted to distinguish grouped from ungrouped responses in this type of experimental situation. As the decision to respond to "both" stimuli is supposed to involve a single decision process, the grouped responses should be made together provided that there is no additional source of delay. Simultaneity of response is, therefore, one criterion. This simultaneity need not be absolute, since differences in conduction time in the two peripheral motor pathways will still appear. But similar differences should be found in the control mean reaction times of the two responses performed separately.

Another criterion would be the preponderance of long RT_1's associated with short RT_2's at the early intervals. This includes as "grouped" not only simultaneous responses but those responses where no "refractoriness" has occurred, and where there is evidence of waiting or straying of the attention at the time of S_1. Davis (1956) employed this criterion, calculating the product moment correlation coefficient between the reaction time of each of his pairs of responses.

The method adopted in the present paper is to plot the pairs of responses in the form of a scattergram (see Figs. 3 to 5) and to examine it for a bimodal distribution. "Grouped" responses should be clustering around the diagonal representing simultaneous response ($RT_1 = RT_2 + I$), while the ungrouped responses, which are expected to show long RT_2's, will be on the right-hand side of the diagonal which represents equal RT's.

There is a further characteristic which may be expected of grouped responses. Hick and Welford (1956) appear to regard the essential thing about the situation in which grouping occurs as the inability reliably to resolve the order of the two stimuli. Grouping can be expected at "all intervals less than the least at which the *order* of the two successive events is reliably distinguished; it is not sharply defined, but is well known to be in the region of 50 to 100 millisec." One may conclude that, other things being equal, grouped responses should occur in the wrong order roughly as often as they do in the right one.

If the intermittency hypothesis is to be accepted in its present form, two nearly simultaneous stimuli must either be grouped and treated as a single situation, or one of the two must be ignored until the decision process to the other is finished. The necessity for using a single central mechanism would not in any case allow independent responses to be made in each case.

The present experiment was designed as a critical test of this prediction. The subject was presented with a situation in which the stimuli (when they both occurred) were always nearly simultaneous, so that there was every chance for him to show "grouping" of responses, while, if he did not do so, "blocking" of the second response would be pronounced and readily detectable. The two stimuli were arranged to occur within 50 or 100 millisec. of each other, and there was a high probability (0·75) of them both occurring. By using paired and unpaired stimuli at only two intervals, a great deal more intensive practice was possible than in similar experiments with a larger number of intervals, and the practice was more evenly distributed between first and second responses at any particular interval.

Method

The apparatus was similar to that used by Elithorn and Lawrence (1955). The subject sat 2·5 metres from a black bakelite screen, 61 cm. square, on which were set, 25 cm. apart, two clusters of five miniature neon bulbs. Mid-way between them was a fixation point, which could be illuminated from behind to provide a warning signal. The subject's hands rested on two keys, operating with a pressure of approximately 400 gm. Each stimulus was a 10 millisec. flash of one neon cluster, and the subject was required to respond as quickly as possible by pressing the left-hand key after the left stimulus and the right-hand key after the right stimulus.

Stimuli were presented within a period of 100 millisec.; the warning light came on 1200 millisec. before the beginning of this period and remained on for 800 millisec. The stimulus situations were presented every 4 sec., and in each situation either one or both stimuli could occur. The presentation of each stimulus and the order of presentation was decided by partial randomization with the following restrictions. Each stimulus (left and right) occurred with equal frequency at one of three times, 0, 50 or 100 millisec. after the end of the 1200 millisec. warning period, but the two stimuli were never presented simultaneously. In one situation in four either the left or right stimulus was omitted, so that only one stimulus occurred. In the paired stimulus situations there were thus six possibilities: L0/R50, R0/L50, L50/R100, R50/L100, L0/R100, R0/L100. In the first four of these situations the two stimuli are separated by an interval of 50 millisec., but the foreperiod is 50 millisec. longer in the second pair. In the last two situations the interstimulus interval is 100 millisec., and the foreperiod is the same as for the 0/50 situation. In a quarter of the situations where there was only a single stimulus there were again six possibilities: L0, R0, L50, R50, L100, R100. The order in which the various situations were presented was randomized within runs of 24 and programmed automatically by punched tape. To minimize the risk of the subject using the restricted randomization as a clue to the last few responses in each run (e.g. by counting the number of single situations), the stimuli were presented, not in blocks of 24, but in runs of 32 straddling the blocks. Daily sessions consisted of 96 situations (4 blocks) divided into 3 runs of 32 situations each, with a few minutes' rest between runs. Two subjects, both right-handed, completed 18 sessions (1,728 situations) without knowledge of results. At that time, the second subject, who had shown a most interesting bilaterally asymmetrical pattern of responses, was asked to continue the experiment. He went on to complete a total of 42 sessions (4,032 situations).

Certain abnormal responses have been excluded from the results. Premature responses can be of two kinds: those completed before the stimulus on the corresponding side and those initiated prematurely but not completed until after the stimulus appears. The latter appear as if they were short reaction times. In the present experiment all responses with reaction times less than 100 millisec. were omitted from the calculation as being almost certainly premature. The number, which was small, is given in Table I Similarly, the relatively few disproportionately long reaction times of more than 500 millisec. (usually associated with missing the key) have been omitted. The apparatus itself recorded premature responses made before the stimulus. These automatically stopped the presentation of further stimuli and lit one of two red bulbs located on either side of the display.

There were no designated practice periods and all the responses were recorded. Practice effects will be reported and discussed. It is worth emphasizing, therefore, that the number of responses made by our subjects (3,024 and 7,056 respectively) is high compared with that reported by most previous workers, even when practice periods are included. Moreover, this total number is distributed between a smaller number of different situations.

Results

There were three possible stimulus times for each hand, viz. immediately after the foreperiod, 50 millisec. later and 100 millisec. later (time "0," "50" and time "100" respectively). Further, at any particular time the stimulus might occur alone or with another stimulus contralaterally at either of the other two possible times. The mean reaction times to a stimulus occurring at each of the three times ("0," "50" and "100") are plotted for the left and right hands of Subject I in Figure 1 and for Subject II in Figure 2. At each time, the three possible situations (alone or with a contralateral stimulus at one of the two other times) are plotted separately. To show practice effects the means are presented for successive 6-day periods. A striking effect of this kind is seen in the period-to-period changes of mean RT_1 (Figs. 1 and 2, open symbols). In both subjects the left hand tends to start much slower in its responses than the right and to speed up later, apparently at the expense of the right hand. The latter (at least initially) becomes slower in responding and even at the end of the experiment is never appreciably faster than it was in Period 1. In contrast to this asymmetry in the first or single responses, there is much less difference between the speed of response of the two hands to a second stimulus (Figs. 1 and 2, filled-in symbols). All the second responses of Subject I tended to speed up with practice. Subject II, on the other hand, showed a sudden slowing down of his second responses, unaccompanied by any comparable change in RT_1, at the time he was told that he had to continue the experiment for a further period. This effect is similar and equally marked for both hands. The occurrence of apparently independent changes in the speed of first or second responses in the same hand is a remarkable feature of these results.

Apart from practice effects, the second subject in his longer experiment also shows some less consistent period-to-period fluctuations in mean RT, rather similar for both hands and at all the times. Both subjects show some differences in speed of response at the different times. Except for Subject II's right hand, there is a consistent tendency for RT_1 to be faster at the later times.

Performance in the double stimulus situation: RT_1 and RT_2 compared

It is clear from Figures 1 and 2 (open symbols) that there is little or no difference between the speed of response to a stimulus occurring first, whether it is subsequently followed by a second stimulus or not. This forces the conclusion that single stimuli are being treated in the same way as if they were "firsts," but does not exclude the possibility that waiting to see if a second stimulus is coming may be artificially inflating the RT in both situations. It does suggest, however, that if there is any waiting it must be for approximately the same period in all three cases. Unfortunately, the possibility of concealed waiting means that RT_1 is not a truly effective measure of "normal" RT_2 (RT_N), and this must be borne in mind in assessing the amount of delay in RT_2. The delay may appear to be smaller than it actually is.

Since mean reaction times may not accurately reflect the pattern of individual responses, the RT's for individual pairs of responses were plotted for each 6-day period. Eight of these scattergrams are shown in Figures 3 to 5. Reaction times to the first stimulus of each pair are plotted along the Y axis, and to the second along the X axis. The responses to the corresponding single stimulus situations are shown as histograms lying along these axes. The three diagonals drawn in each scattergram represent three possible time relationships between the pairs of responses: namely, first and second responses made simultaneously, responses in which

FIGURE 1

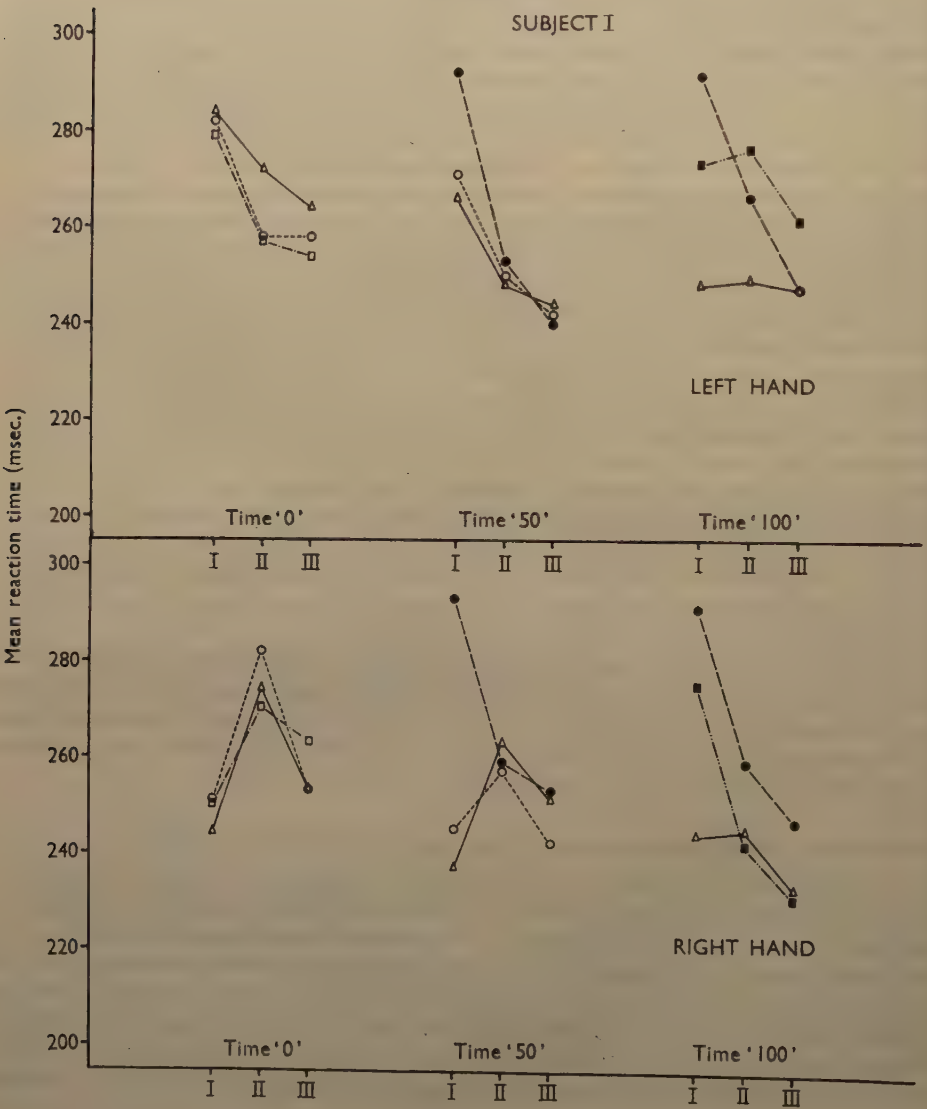
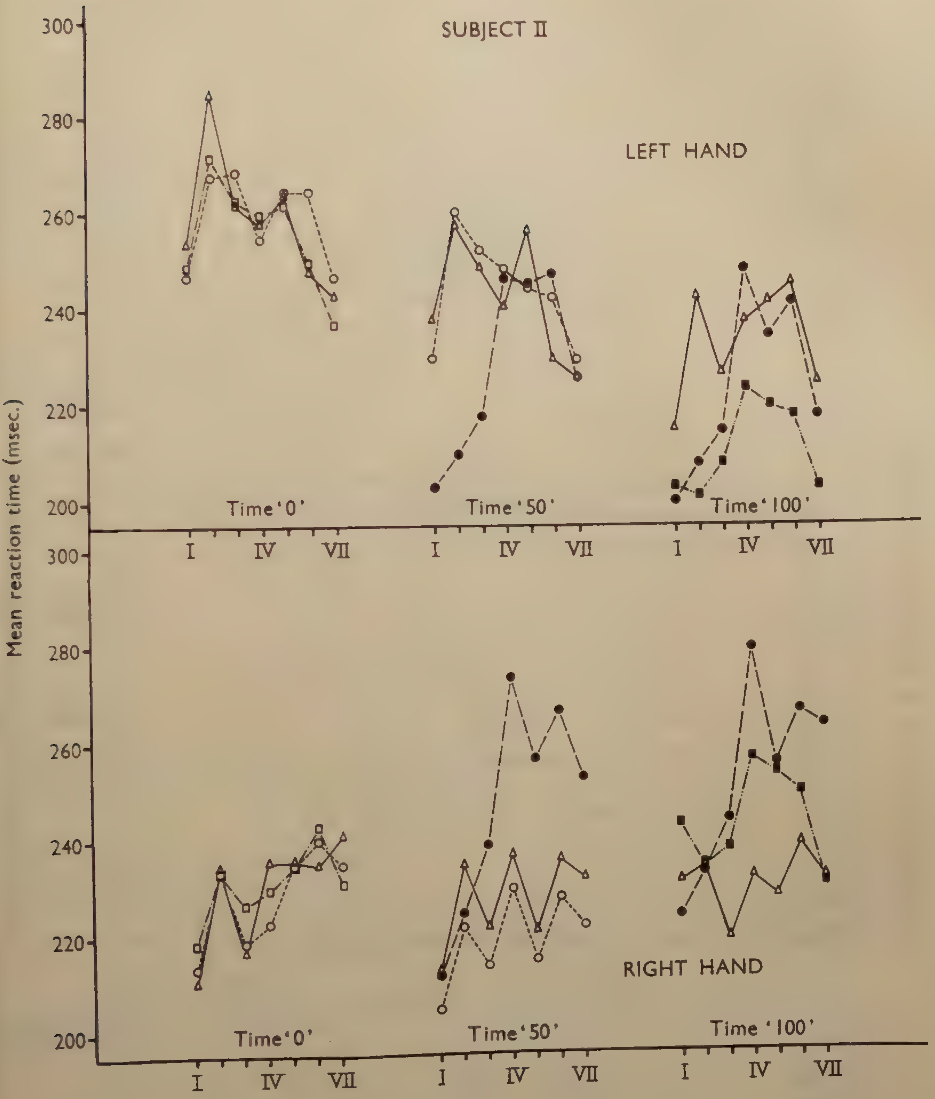


FIGURE 2



FIGURES 1 and 2

Mean reaction time of each hand for successive 6-day periods of the experiment (I, II . . ., etc.) to stimuli occurring at each of three possible times, viz. immediately after the foreperiod (time "0"), 50 millisec. later (time "50") and 100 millisec. later (time "100"). Figure 1 shows mean RT's during the three 6-day periods completed by Subject I. Figure 2 shows mean RT's during the seven 6-day periods completed by Subject II.

In Figures 1 and 2 the following conventions are adopted. Means of the responses to *single* or *first* stimuli are shown in *open* symbols; those to *second* stimuli in *filled-in* symbols. *Circles* indicate responses with an interstimulus interval of 50 millisec.; *squares*, *100* millisec.; *triangles*, a single stimulus situation.

FIGURE 3

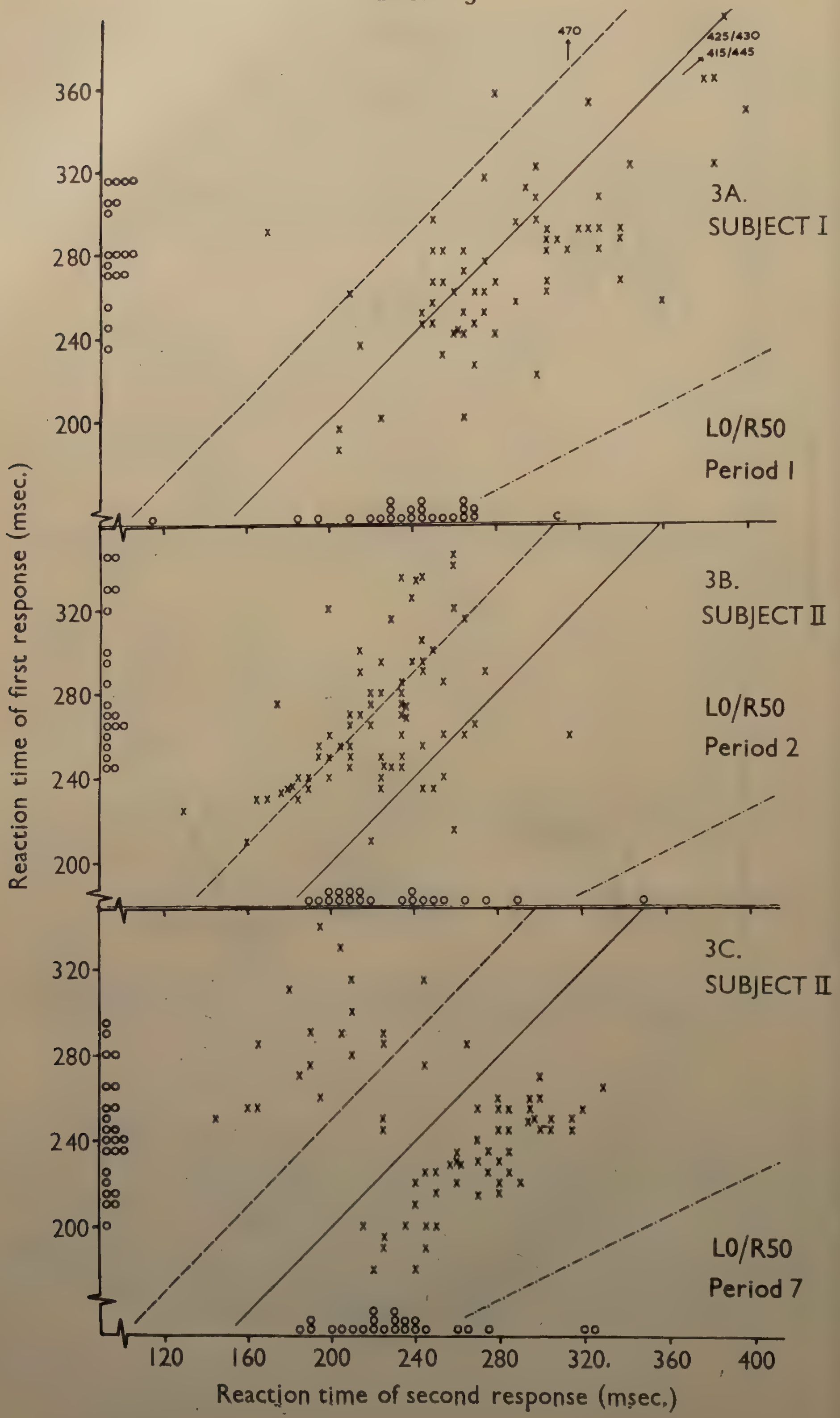

470
425/430
415/445
3A.
SUBJECT I
L0/R50
Period 1
3B.
SUBJECT II
L0/R50
Period 2
3C.
SUBJECT II
L0/R50
Period 7
360
320
280
240
200
120
160
200
240
280
320
360
400
Reaction time of first response (msec.)
Reaction time of second response (msec.)

FIGURE 4

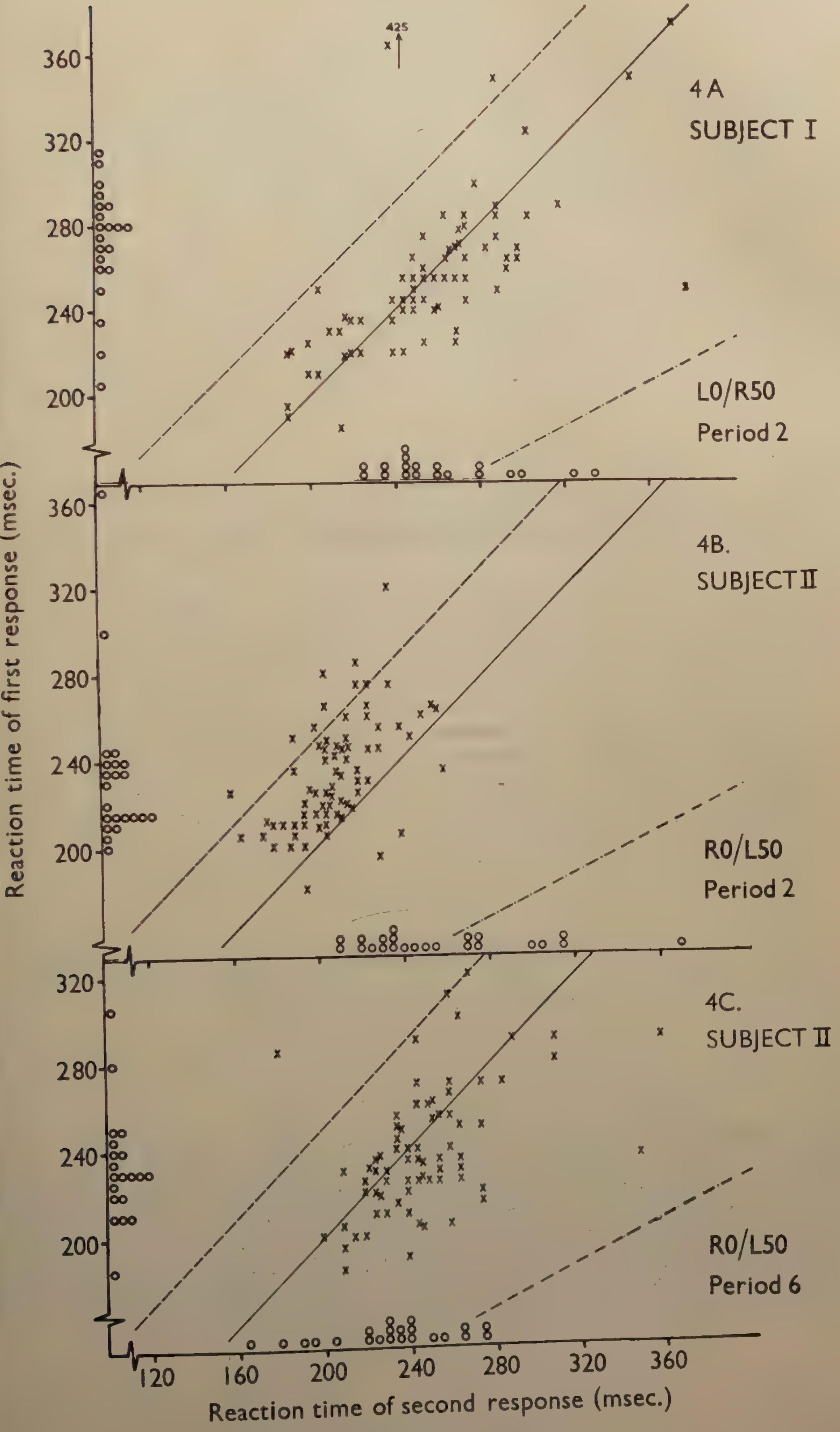
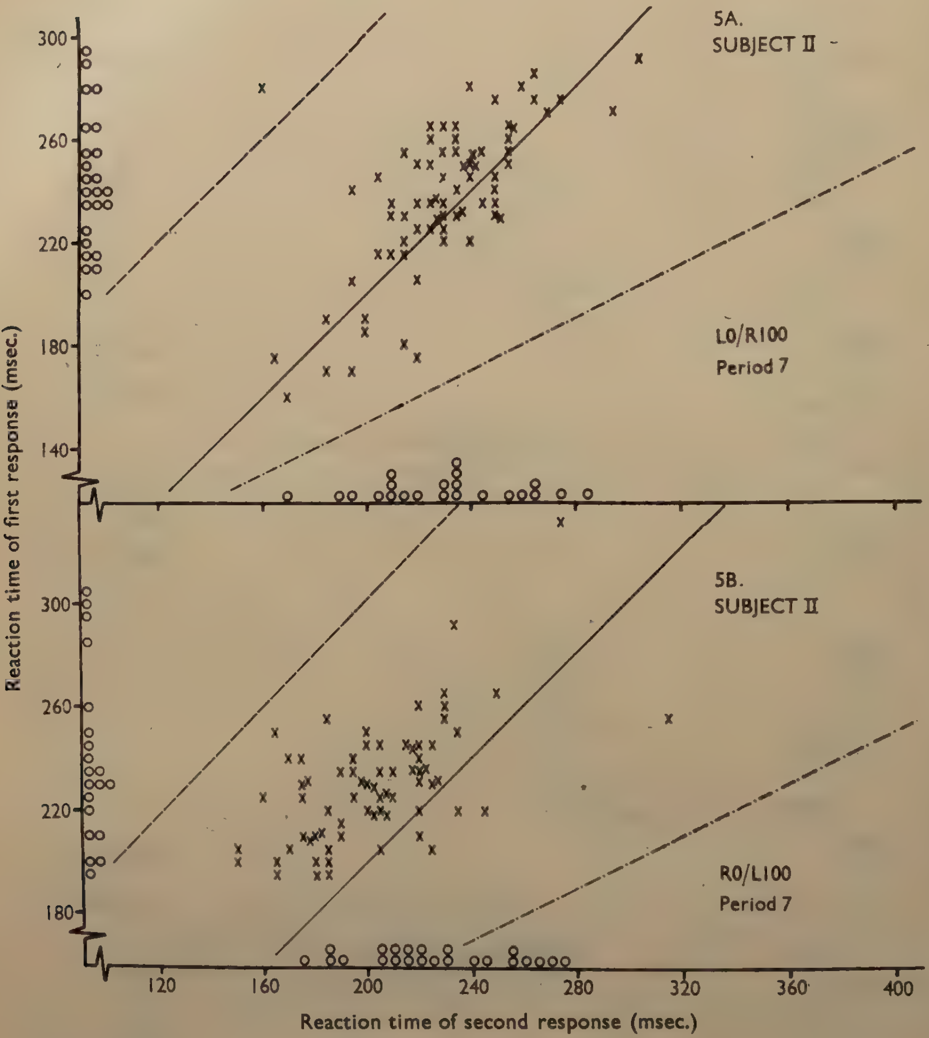

425
4 A
SUBJECT I
L0/R50
Period 2
4B.
SUBJECT II
R0/L50
Period 2
4C.
SUBJECT II
R0/L50
Period 6
360
320
280
240
200
120
160
200
240
280
320
360
Reaction time of first response (msec.)
Reaction time of second response (msec.)

FIGURE 5



FIGURES 3 to 5

Scattergrams for all individual pairs of responses in a particular 6-day period of the experiment. RT_1 is plotted along the ordinate, RT_2 along the abscissa, and the RT's to the corresponding single stimulus situation at the same time for the same hand are shown as histograms lying along the axes. The solid line diagonal indicates *equal* RT_1 and RT_2 ("independence"); the interrupted diagonal to the left of this represents an RT_1 exceeding RT_2 by the interval ("waiting and grouping"), both responses being made simultaneously; the dotted diagonal to the right of the scattergram represents an RT_2 delayed with respect to RT_1 by the amount (RT_1 — I) ("central intermittency").

$RT_1 = RT_2$ and responses in which RT_2 exceeds RT_1 by $RT_1 - I$. Grouped responses which are made nearly simultaneously will lie along the interrupted diagonal to the left, while independently organized responses should reproduce the interstimulus interval and lie close to the solid diagonal of equality. The intermittency model put forward by Davis does not permit one to predict the line about which the delayed second responses should lie, unless assumptions are made about the proportion of the reaction time which should be attributed to central processes. The third diagonal on the extreme right of each diagram therefore illustrates the relationship predicted by the intermittency hypothesis as formulated by Welford, in which RT_2 is prolonged by a delay equal to $RT_1 - I$.

The procedure adopted was to examine the means of the double responses for indications of grouping, delay or independence, and to compare these with the appropriate scattergram for confirmation. This approach yielded interesting results, and the following situations have been chosen to illustrate the varied patterns of responses which can co-exist in the same subject in different situations, or in different subjects in the same situation.

Example I

Mean RT's for Subject I in the situation Lo/R50 are respectively 282 and 293 millisec. (Period 1) and 258 and 259 millisec. (Period 2). These would suggest that RT_2 is being delayed relative to RT_1 only slightly in Period 1 and that by Period 2 the two responses have become virtually independent. Reference to the corresponding scattergrams (Figs. 3A and 4A) show that this is substantially true. In neither period are the observations far from the line of equal RT though the scatter is greater in Period 1 and several points are in excess of the single "control" responses at R50. By Period 2 many of the points are on or near the line of equality. The mean RT_2 of 259 millisec. is less than the corresponding mean for the single responses (R50 alone), which makes it unlikely that the pattern of response here is due to the introduction of a deliberate delay in RT_2. The mean RT_1 at 258 millisec. is also well below the equivalent single response (Lo alone) and is in line with RT_1's at the same interval in other situations. There seems to be considerable evidence here that responses to two stimuli at this interval have been dealt with independently.

Example 2

The mean RT's for Subject II in the same (Lo/R50) situation in Period 7 are respectively 247 and 252 millisec., which again suggests independence. The scattergram (Fig. 3C) shows, however, that the means are derived from a bimodal distribution in which about one-third of the paired responses are reversed, i.e. made with the right hand first, and the other two-thirds are subject to appreciable delay. The impression of equality given by the means is therefore misleading. This clear-cut bimodal distribution was confined to Subject II and to the latter stages of the experiment and was only found in the left/right sequence of responses. It appears in a modified form in the other 50 millisec. interval situation (L50/R100), which is not illustrated here. Earlier in the experiment (Period 2) the means are markedly different (Lo—268, R50—224) and suggest grouping. The scattergram (Fig. 3B) confirms this as almost all the responses are above the line of equal response and many are actually reversed. There is no evidence of the bimodality which develops later. Subject II obviously found it very difficult to make independent responses in this situation.

Example 3

In the right/left sequence, however, Subject II appears to be readily capable of independent organization. The mean RT's for the situation Ro/L50 in Period 6 are 239 and 248 millisec. respectively. The suggestion of independence is confirmed in Figure 4C, in which there is little grouping and a few delayed responses, but most of the observations lie along the line of equality. As in the previous example, however, the means for Period 2 (234 and 210 millisec.) imply a tendency to group responses and this is confirmed in Figure 4B, though even here many of the pairs of responses are nearer to equality than to simultaneity. With practice this subject is clearly able to solve the grouping problem in the right/left sequence and achieve independent responses, whereas the avoidance of grouping in the left/right sequence leads to the appearance of delayed RT_2's.

Example 4

The analysis so far has been confined to the 50 millisec. interval. The means for the 100 millisec. interval situation (Period 7, Subject II) show a similar final response pattern whichever stimulus comes first. RT_1 exceeds RT_2 by 27 millisec. in the Ro/L100 situation and 7 millisec. for Lo/R100. The scattergrams (Fig. 5) show that in the sequence with the greatest difference (Ro/L100) the individual responses are made in a fairly consistent pattern with RT_2 generally less than RT_1, but they are clustered much nearer the line of equality than that of simultaneity.

Performance in the double situation: the pattern of delayed responses

It is obvious from inspection of the mean reaction times that there are many occasions in which RT_2 is delayed relative to RT_1. Nowhere, however, are the delays of the magnitude predicted by Welford's hypothesis ($RT_1 - I$). Table I shows that the greatest mean delay shown by either subject in the whole experiment is 47 millisec. (Subject I, Period 1, R50/L100). The corresponding scattergram (not illustrated) shows that the distribution of responses was fairly homogeneous, with very few grouped responses so that the size of the delay is not masked by a number of artificially high RT_1's and low RT_2's. This can be checked by calculating the mean delay of the delayed responses alone. When these alone are included in the calculations, the amount of delay only increases to 61 millisec.

It is worth studying more closely the nature of these delays. The delayed responses shown in Figure 3C, previously mentioned in Example 2, form a clearly discrete group. Here, too, the delay is much smaller than would be predicted by Welford's formula, the responses being well to the left of the right-hand diagonal in the scattergram. Mean delay of these responses is actually 44 millisec. There is a close relationship between RT_1 and RT_2 ($r = 0{\cdot}79$) but not between RT_1 and the delays ($r = 0{\cdot}14$). In other words, the delay is not proportionately greater when RT_1 is long than when RT_1 is short.

Quite apart from the absolute size of the delay, there is another important discrepancy in the relative amount of delay at the different interstimulus intervals. According to all the variants of the intermittency theory this should be 50 millisec. less for an interstimulus interval of 100 millisec. than for the 50 millisec. interval. Unlike the absolute delay this *difference* should remain unaltered even if there is a constant amount of waiting in both situations altering the value of RT_1 and is not affected if some other function than total RT_1 is taken to represent the central organizing time. It should still be the same even if a substantial part of RT_1 is due to peripheral conduction time, provided that the central organizing of the first response

TABLE I

SUBJECT I

Stimulus situation	*Period*	*Mean RT for left hand*	*Mean RT for right hand*	*N**	*No. of premature responses*	*Responses outside range*	*Errors in recording*
R alone at 0	1	–	244·5 ± 6·4	21		–	–
	2		274·1 ± 7·3	22	2		
	3		253·9 ± 4·9	19	2		
L alone at 0	1	283·9 ± 5·9	–	18	2	–	–
	2	272·1 ± 6·0		21	3		
	3	263·9 ± 4·8		22	1		
R alone at 50	1	–	237·5 ± 7·6	24		–	–
	2		263·2 ± 7·3	19	3		
	3		251·6 ± 7·5	22	1		
L alone at 50	1	265·8 ± 6·8	–	20	4	–	–
	2	247·6 ± 3·8		19	4		
	3	243·9 ± 4·7		23			
R alone at 100	1	–	243·6 ± 6·7	25		–	–
	2		245·2 ± 4·3	25	1		
	3		232·9 ± 7·3	21	4		
L alone at 100	1	248·5 ± 7·6	–	26		–	–
	2	249·1 ± 7·6		23	1		
	3	247·1 ± 6·5		22	1		
Ro L50	1	292·5 ± 5·5	251·0 ± 5·1	67	–	2	
	2	253·6 ± 4·3	282·1 ± 7·5	70		2	
	3	240·1 ± 3·3	253·0 ± 4·3	70		1	1
Lo R50	1	282·0 ± 6·4	293·0 ± 6·5	67	–	2	1
	2	257·6 ± 5·0	259·4 ± 4·7	71		2	
	3	257·9 ± 3·6	252·9 ± 4·0	71			1
R50 L100	1	291·6 ± 5·8	244·9 ± 3·9	63	–	1	
	2	265·8 ± 4·9	256·8 ± 4·0	71		1	
	3	247·5 ± 5·6	242·3 ± 3·6	66		1	2
L50 R100	1	271·3 ± 7·1	291·1 ± 7·8	66	–	2	1
	2	250·1 ± 3·3	259·4 ± 4·2	69			1
	3	242·1 ± 3·5	247·0 ± 4·5	68		1	
Ro L100	1	273·4 ± 6·1	249·7 ± 2·7	70	–		
	2	276·5 ± 5·9	270·4 ± 4·2	68		3	1
	3	261·0 ± 8·2	263·6 ± 4·0	66		1	3
Lo R100	1	279·4 ± 4·3	274·7 ± 5·4	71	1		
	2	257·1 ± 3·2	241·8 ± 5·8	68		2	1
	3	253·9 ± 2·8	231·1 ± 4·9	66		1	

* Number of responses used in all calculations, excluding those in the following three columns.

TABLE I (*contd.*)

SUBJECT II

Stimulus situation	*Period*	*Mean RT for left hand*	*Mean RT for right hand*	*N**	*No. of premature responses*	*Responses outside range*	*Errors in recording*
R alone at 0	1	–	210·0 ± 7·1	16	7	–	1
	2		233·9 ± 7·7	22	2		
	3		216·3 ± 4·1	20	2		2
	4		235·7 ± 6·2	22	2		
	5		235·5 ± 6·4	21	3		
	6		233·8 ± 5·7	20	4		
	7		240·0 ± 7·5	20	4		
L alone at 0	1	254·2 ± 9·5	–	20	3	–	1
	2	285·0 ± 7·6		19	5		
	3	262·5 ± 6·1		22	2		
	4	258·4 ± 4·8		22	2		
	5	264·0 ± 5·3		20	4		
	6	248·1 ± 7·1		24			
	7	243·5 ± 5·3		24			
R alone at 50	1	–	211·8 ± 8·8	22	2	–	–
	2		233·8 ± 8·2	21	3		
	3		221·5 ± 5·5	20	4		
	4		236·1 ± 6·2	22	2		
	5		219·8 ± 6·2	23	1		
	6		226·3 ± 9·5	23	1		
	7		231·3 ± 6·9	24			
L alone at 50	1	238·1 ± 8·7	–	21	3	–	
	2	258·0 ± 8·3		23	1		
	3	249·3 ± 6·0		21	1		2
	4	245·2 ± 4·9		24			
	5	256·7 ± 6·2		24			
	6	230·2 ± 6·1		22	2		
	7	235·5 ± 7·0		21	3		
R alone at 100	1	–	229·7 ± 7·7	19	5	–	–
	2		232·9 ± 7·5	22	2		
	3		218·3 ± 5·3	23	1		
	4		230·9 ± 8·3	23	1		
	5		228·3 ± 5·9	24			
	6		238·3 ± 7·1	23	1		
	7		230·7 ± 6·1	22	2		
L alone at 100	1	214·7 ± 8·4	–	20	4	–	–
	2	242·9 ± 6·7		22	2		
	3	231·4 ± 5·6		21	3		
	4	237·9 ± 7·5		24			
	5	238·0 ± 4·9		23	1		
	6	246·0 ± 9·6		24			
	7	225·4 ± 5·9		23	1		

* Number of responses used in all calculations, excluding those in the following three columns.

TABLE I (*contd.*)

SUBJECT II

Stimulus situation	*Period*	*Mean RT for left hand*	*Mean RT for right hand*	*N**	*No. of premature responses*	*Responses outside range*	*Errors in recording*
Ro L50	1	203·2 ± 3·8	213·1 ± 3·3	70	1		1
	2	210·3 ± 2·4	233·5 ± 2·7	72			
	3	217·8 ± 3·7	218·5 ± 3·6	71			1
	4	247·0 ± 3·3	222·4 ± 2·8	72		–	
	5	246·0 ± 4·4	233·7 ± 3·7	72			
	6	247·9 ± 3·5	239·2 ± 3·5	72			
	7	226·2 ± 3·2	233·9 ± 3·7	72			
Lo R50	1	246·9 ± 4·3	211·3 ± 4·9	72			
	2	267·7 ± 3·6	224·1 ± 3·7	72			
	3	268·8 ± 4·2	237·8 ± 5·7	69		1	2
	4	255·1 ± 4·1	273·3 ± 5·6	71	–		1
	5	265·3 ± 4·3	255·6 ± 5·8	72			
	6	265·1 ± 5·9	266·3 ± 4·6	72			
	7	246·9 ± 4·1	252·0 ± 5·3	71			1
R50 L100	1	200·3 ± 3·5	204·5 ± 3·4	71	1		
	2	208·2 ± 2·7	220·7 ± 3·4	72			
	3	214·6 ± 3·3	213·1 ± 3·2	71			1
	4	248·9 ± 3·7	228·8 ± 4·0	70	1	–	1
	5	235·2 ± 3·8	213·7 ± 4·3	72			
	6	242·4 ± 4·8	226·8 ± 4·1	72			
	7	218·2 ± 3·9	221·5 ± 2·6	72			
L50 R100	1	228·7 ± 3·8	223·2 ± 5·1	71			1
	2	261·1 ± 5·0	232·2 ± 3·9	72			
	3	253·5 ± 4·3	243·5 ± 5·7	72			
	4	248·6 ± 3·8	278·7 ± 5·9	71		–	1
	5	245·1 ± 3·9	255·3 ± 5·0	71			1
	6	242·8 ± 4·8	265·6 ± 4·8	72			
	7	229·8 ± 2·8	262·8 ± 5·0	71	1		
Ro L100	1	203·4 ± 5·2	218·2 ± 4·7	71			1
	2	201·4 ± 3·9	233·2 ± 4·4	70	1		1
	3	208·4 ± 3·8	226·4 ± 4·1	67		1	4
	4	224·4 ± 3·7	229·4 ± 3·6	72			
	5	219·6 ± 4·1	234·0 ± 4·9	72			
	6	218·3 ± 3·9	242·2 ± 3·8	72			
	7	203·0 ± 3·5	229·9 ± 3·1	70	2		
Lo R100	1	249·2 ± 3·8	241·7 ± 3·1	68	2	1	1
	2	272·0 ± 3·7	232·7 ± 3·9	69	1	1	1
	3	263·4 ± 3·7	237·2 ± 3·6	71	1		
	4	259·7 ± 3·4	256·3 ± 3·4	72			
	5	262·3 ± 4·2	252·6 ± 3·8	71			1
	6	250·5 ± 3·8	249·6 ± 4·5	71			1
	7	237·2 ± 3·4	229·9 ± 2·8	72			

* Number of responses used in all calculations, excluding those in the following three columns.

time is not less than 100 millisec. A further factor must be considered. As Elithorn and Lawrence (1955) pointed out, the expected RT_2 cannot strictly be inferred from the observed RT_1, since the arrival of the first stimulus changes the subject's set in relation to the second. The arrival of S_1 converts the originally disjunctive situation into a simple response. Leonard (1958) has confirmed that advance information of this type can be used more effectively to speed up a reaction time to a second stimulus as the interval between stimuli increases. This means that the expected RT_2 will be reduced as the interval increases. In the present case this would increase the difference between the delays shown at the 50 and 100 millisec. intervals, i.e. $(RT_2 - RT_1)_{50} - (RT_2 - RT_1)_{100}$. A comparison of these delays shows that the reduction at the longer intervals is often much less than the 50 + millisec. predicted by the combination of Welford's theory and Leonard's observation. The observed differences range from a minimum of 0 millisec. (Subject II, Period 6: L0/R50 and L0/R100) to a maximum of only 40 millisec (Subject II, Period 7: L50/R100 and L0/R100).

Discussion

The data here presented show beyond question that even with two stimuli separated by only 50 or 100 millisec. it is possible to make second responses which are as fast as those made to a single stimulus, but are not performed almost simultaneously with the first response, as would be expected were they being grouped. Before accepting the view that these undelayed second responses are truly independent (in the sense of being made separately, in response to the second stimulus, after the central processes concerned in the first response are already under way) two possibilities need to be considered, viz. (1) that they are premature responses, initiated before the arrival of the stimulus, but masked by its subsequent occurrence, and masquerading as genuine responses shorter than they really are; and (2) that they represent a special kind of concealed grouping, in which the responses are made, not simultaneously, but one after the other in the right order and at the right interval, as the outcome of a single "decision process."

The design of the experiment might have been expected to lead to an appreciable number of premature responses, since stimulus probability was high over a very short range of time and guesses as to which side the stimulus was coming have never less than a 50 per cent. chance of being right. However, an index of the percentage of premature responses occurring is given by the number recorded on the 25 per cent. of occasions when there was no stimulus on one of the two sides. The number and distribution of these is recorded in Table I: Subject I had 29 in 421 situations (6·9 per cent.) and Subject II 86 out of 1008 (8·5 per cent.). Premature responses may be made on a particular side either before S_1 has arrived or after a contralateral S_1 in anticipation of an S_2. Since both these types of premature response contribute to the percentage figures for the single stimulus situation calculated above, it seems reasonable to assert that less than 9 per cent. of the second responses on each side can be premature. Such a percentage clearly cannot account for the very large proportion of undelayed second responses, performed with a reaction time almost equal to that of the first response.

The second possibility is more difficult to exclude, but there are reasons for regarding it as equally unlikely. The suggestion is that the subject might be grouping the responses in a rather sophisticated way, and deciding to do them, not simultaneously, but in the correct sequence and at an interval corresponding to that between the two stimuli. As only a single decision process is involved, the intermittency hypothesis is still satisfied, although grouping can no longer be regarded as something which occurs when the order of the two stimuli cannot be reliably distinguished. In the pattern of undelayed second responses the order and the interstimulus interval are not only distinguished but accurately reproduced (e.g. Figs. 4A and 5A).

In the model proposed by the intermittency hypothesis, the single decision process to respond to both stimuli cannot begin until the second stimulus has arrived. It is supposed that the grouping decision may be either to respond to both stimuli at the same time, or to respond to them consecutively at the interstimulus interval. In the first case RT_1 must have the interstimulus interval added to it; and in the second, both RT_1 and RT_2 will be increased by this amount.

As RT_1 must exceed the true reaction time by the interstimulus interval, it can only be equal to its control RT_1 (i.e. any *un*grouped first response) if there is *always* the same amount of waiting whether the responses are grouped or not. In the present experiment there is no appreciable difference in the mean RT_1's whether a second stimulus follows in 50 or 100 millisec. or not at all. Clearly, then, the amount of waiting (if any) must be the same in all cases. The subject could produce the supposedly grouped pattern of equally fast responses with stimuli 100 millisec. apart (Fig. 5), but there is no evidence that his RT_1 was quicker when both stimuli had already arrived by time "50." Assuming that grouping is occurring, it is difficult to explain why it is not 50 millisec. shorter in the latter case unless he is waiting a further 50 millisec. after *both* stimuli have arrived.

Further, if the subject always waits 100 millisec. before initiating his response, his true reaction time for both grouped responses (subtracting 100 millisec. waiting) would be of the order of 100 to 150 millisec. and at the 100 millisec. interstimulus interval for Subject II about 110 millisec. (Fig. 5). Even a simple visual reaction time is of the order of 150 millisec. and the present situation is a disjunctive one Moreover, if the grouping strategy is adopted, the situation becomes at least a three-choice one, and theory predicts that the reaction time should be considerably longer (Hick, 1952; Hyman, 1953; Welford and Hick, 1956). Some support for these doubts is also provided by an experiment of Hick (1948) in which the subject was instructed to try and group his responses. In the responses regarded by Hick as grouped, RT_2 was almost always longer than it was for the ungrouped second responses, even though refractory delays were occurring in the latter. The mean "complex" reaction time was about 430 millisec. as against 389 millisec. for the ungrouped.

In the present results, on the other hand, RT_2 is considerably *faster* than its control when the supposedly grouped patterns of responses are occurring. This applies both to the mean RT_2 (e.g. Subject II's left hand, Fig. 2) and the individual second responses (Figs. 4B and 3C). RT_1 in these responses, far from having the interstimulus interval added to it by waiting, is no longer than its own control or of the control RT_2. Instead of RT_1 being longer by the interstimulus interval and RT_2 equal to its control, RT_1 is unchanged and RT_2 has been speeded up. This may, of course, represent some degree of waiting in all the responses to S_1, but it is evident that any such waiting is in no sense peculiar to the periods when the subject is producing nearly simultaneous first and second responses, and it can hardly be of the order of 100 millisec. in all cases.

These results therefore appear to be incompatible with the suggestion that all apparent exceptions to the lengthening of the early second reaction time predicted by the intermittency hypothesis are due to grouping of responses. A large number of those second responses were not delayed, but were performed as fast as the first responses, and their timing makes it almost impossible that they can be the outcome of a single decision process as envisaged by the single information channel model. Where the two responses were made nearly simultaneously, the second is faster than its control, and where they were made in the right order at the right interval, the second was roughly equally fast as its control; in neither case was RT_1 significantly different from its control, and its low value precludes the possibility that much waiting was occurring.

There remain the delayed second responses to be considered, and these, too, do not appear to fit easily into the framework of the intermittency theory. There are two reasons for this. Firstly, the delays were never of anything like the magnitude predicted by the $RT_1 - I$ relationship (even if due allowance is made for the conduction time in the motor pathways), and, secondly, they were largely learnt out by one of the two subjects in the course of the experiment. It seems that there must have been something in the present experimental situation peculiarly favourable to this, because it has been the experience of earlier workers that these delays are resistant to training (Hick, 1948; Davis, 1956, 1957; Marill, 1957). But Telford (1931) and Elithorn and Lawrence (1955) have previously noted that they were reduced by practice and this has recently received strong support from a study by Mowbray and Rhoades (1959), who have shown that the initially greater RT in a four-choice situation as compared with a two-choice one can be eliminated with sufficient practice. The present experiment differs from many of these earlier ones in the much greater probability of S_2 occurring 50 or 100 millisec. after S_1 and the much more intensive practice which the subjects had in responding at these times. This results from the choice of only two interstimulus intervals; where a larger range is used, each has to be presented and there will inevitably be a proportionately lower expectancy of S_2 occurring at any particular interval after S_1. It seems a reasonable surmise that the high expectancy for S_2 may account for both the shortness of the delays observed and their disappearance with training.

Welford (1952) considered the possibility that the delays in early RT_2's might be due to the unexpectedness of S_2 soon after S_1; his main reason for rejecting it was the belief that they were not reduced by practice. Hick (1948) also came to the conclusion that there were irreducible delays associated with the second of two closely-following responses. The present results, however, show that they are not inevitable, and also that they do not necessarily have an all-or-none character.

There are thus many important features of the pattern of responses in these experiments which make any attempt to fit them into the intermittency hypothesis somewhat of a Procrustean labour. This is by no means to deny that there is some form of interaction between the two central processes concerned in the two responses; it is only to deny that such interaction is limited to their being either combined in a single process (grouping) or whichever is first blocking the second until it is finished (intermittency). The present findings point to a central mechanism of considerably more plasticity. The second response, even when called upon within a few milliseconds of the first, may be apparently speeded up, slowed down or made at the same speed. The actual pattern was not necessarily the same on both sides and seemed to depend in our subjects on the *order* in which the two sides were called upon to respond.

It may be concluded that, whatever the explanation of the delayed responses upon which the idea of the "psychological refractory period" is based, the latter is not a necessary or invariable phenomenon. There is, in fact, strong evidence against any inevitable intermittency in the central mechanisms concerned with the responses to two nearly simultaneous stimuli.

Our thanks are due to Miss J. Mott and Miss R. Mingay for their help in carrying out the experiments and preparing the results for publication, and to Dr. E. A. Carmichael for his support and encouragement.

Note: While this paper has been in press, a further paper by Welford has appeared (this *Journal*, **11**, 193–210), which contains a detailed discussion of grouping of stimuli and the single channel hypothesis.

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STUDIES IN OLFACTORY ACUITY. I.

Measurement of Olfactory Thresholds in the Rat

BY

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The capacity of the rat to respond to olfactory cues has been studied in three experimental situations: (i) an elevated Y-maze, (ii) a rectangular choice apparatus in which extraneous environmental cues were present, and (iii) a circular choice apparatus from which such cues were either excluded or randomized.

No rat showed any sign of learning on the Y-maze even after extensive training and the application of electric shock as deterrent for error.

Some rats succeeded in performing an olfactory discrimination in the rectangular choice apparatus but learning was retarded, and in some cases inhibited, by the counter-influence of non-olfactory factors.

All rats readily learned an identical discrimination when shielded from such cues in the circular choice apparatus which provides a satisfactory medium both for training and for the study of olfactory acuity.

Differences in the behaviour of rats on these three types of apparatus suggest first, that the formation of learned habits based on olfaction depends on the close contiguity of stimulus and reward, and second that the sense of smell possesses weak orientating properties by comparison with those exerted by other modalities. The findings thus help to explain differences in the ease or difficulty with which olfactory discriminations have been established by earlier workers.

INTRODUCTION

The electrophysiological studies of Adrian (1951) together with the work of Guillot (1948) on partial anosmia have suggested that there may be a number of functionally distinct types of olfactory receptor and this view has recently received support on histological grounds (Clark, 1956). But although these findings provide a basis for understanding the way in which the olfactory organ can discriminate between different odours the mechanisms by which odorous substances excite the various olfactory receptors is still far from clear.

A possible approach to this problem is through an analysis of the relationship between the physico-chemical properties of odorants and their relative detectability. Most earlier work on these lines has been confined to a study of olfactory thresholds in man and insects and little attempt has been made to exploit the possibilities of macrosmatic laboratory animals as test subjects. A probable reason for this, at least as far as the rat is concerned, is the obvious difficulty experienced by previous investigators (e.g. Liggett, 1928; Swann, 1933; Brown and Ghiselli, 1938) in developing satisfactory techniques for establishing habits based on olfactory discrimination, for only when the odour of food itself has provided a major component of the positive stimulus has rapid learning been obtained (French 1940; Stone, 1941; Lashley and Sperry, 1943).

It is thus clear that methods which have proved satisfactory for teaching discriminations based on non-olfactory modalities of sensation are unsatisfactory for quantitative studies on olfaction either by reason of the difficulty with which they can be successfully applied or of the restricted nature of the stimuli to which the rat will readily respond. Any alternative must not only overcome these disadvantages but must also ensure that all possibility of response to extraneous cues is eliminated. The methods, for example, of Le Magnen and Rapaport (1951), who trained rats to discriminate between drinking bottles on the basis of odorous substances smeared on to their spouts, and of Gruch (1957) whose rats chose one of three boxes containing food on the basis of odorous or non-odorous air admitted from an associated tube, may be criticized on the ground that visual cues and the smell of the reward were not adequately controlled. The sensitivity of the rat to the odour of food is in fact so keen (Hand, 1952; Le Magnen, 1952) as to effectively rule out its use as a direct reward in experiments designed to estimate olfactory thresholds; for even if controlled (as, for instance, by their presence in relation to both positive and negative stimuli) odorous food molecules may mask the presence of the test substances either by competing for olfactory receptors or by chemical reaction.

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The purpose of the present paper is to describe a method for the study of olfactory acuity in the rat* and, since certain preliminary observations would appear to throw some light on difficulties experienced by earlier workers, to outline the several stages leading to its development. The fuller use of this technique for demonstrating the olfactory thresholds of a series of chemically related compounds is described in the following paper.

MATERIAL AND METHODS

Apparatus

Three different sets of apparatus, designated the (i) Y-maze, (ii) rectangular, and (iii) circular choice boxes were used during the course of the experiments. The initial design and incidental modification of this apparatus were based on experimental observations made during its use and are therefore more conveniently described together with the Results.

Animals

The preliminary experiments reported here were carried out using albino rats of the Birmingham strain. In view of claims that olfactory acuity in man is influenced by the ovarian cycle (Elsberg, Brewer and Levy, 1935; Le Magnen, 1950; Schneider and Wolff, 1955) only male rats were used.

Odorants

The odorants used during these preliminary trials were oil of cloves (eugenol) and hexanol. These were initially dissolved at a concentration of 10 per cent. in propylene glycol, subsequent aqueous dilutions being made by factors of 10. Equivalent dilutions of propylene glycol alone acted as controls. A further series of tests was carried out using aqueous ethanol. No special precautions were taken to eliminate possible contamination.

Mode of estimating thresholds

(*a*) *Conduct of tets.* For reasons described later only the circular choice apparatus was ultimately used to measure thresholds. Rats were motivated by restricting their water intake to about 15 ml. daily and were introduced into the apparatus manually at each trial. Where, as in later trials, the odour to be detected was carried in nylon capsules, these were discarded after use so that no rat was presented with the same capsule more than once.

After preliminary training the approximate threshold for each test substance was determined by conducting a preliminary series of trials based on graded concentrations of odorant ranging from 10^{-1} to 10^{-14} and analysing the data by the method of probits. The range of concentrations ultimately used for testing was centred about the value so obtained for a 50 per cent. success score. Rotation of rats in relation to the sequence of trials resulted in the intervention of an interval of at least 30 sec., and usually longer, between trials for any given rat and this was thought sufficient to minimize the possible effects of adaptation to the odour. Further, in order to minimize the influence of day-to-day fluctuations in performance the concentrations chosen were presented in accordance with a balanced incomplete block design in which all concentrations were replicated the same number of times. The designs used (see Fisher and Yates, 1948) were the 9 × 12 (i.e. 9 dilutions at the rate of 4 per day over 12 days with 3 replications), 7 × 7 (4 dilutions per day with 3 replications) or 16 × 16 (6 dilutions per day with 6 replications).

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* Since the work reported in this paper was completed Pfaffmann, Goff and Bare (1958) have published a technique based on operant conditioning which would appear to meet most of the methodological criticisms outlined and to serve the same end as the method here described.

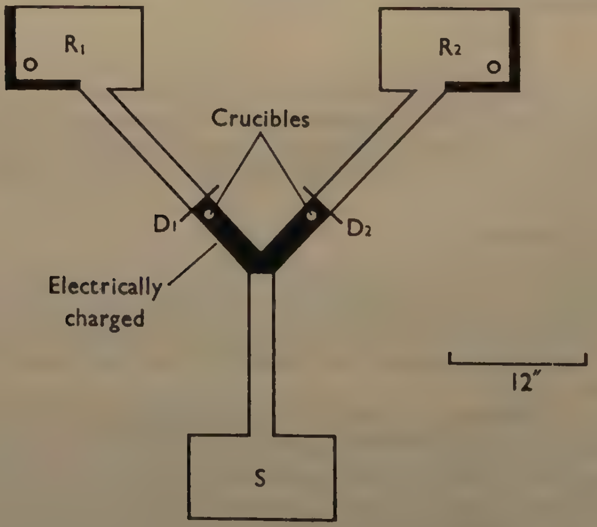
(*b*) *Scoring and treatment of data.* The number of correct and incorrect choices was recorded, and on completion of each block of trails the rectified mean percentage of correct responses at each concentration was computed in accordance with the usual procedure for balanced incomplete blocks (Yates, 1936) and the values so obtained subjected to probit analysis (Finney, 1952). A separate probit regression was computed for each set of data and used to obtain the olfactory threshold in terms of the concentration detectable at the 50 per cent. level. The thresholds thus obtained were expressed as the dilution of the odorant in solution, and since the object of these preliminary experiments was merely to establish the usefulness of a technique, the data were subjected to no further treatment. In later experiments, however, in which a comparison of the relative detectability of different odorants has been attempted, more refined procedures have been adopted (Moulton and Eayrs, 1960).

RESULTS

(*a*) Y-*maze*

The apparatus used (Fig. 1) was similar in general construction to the 3-table apparatus of Maier (1932). A crucible, covered by a copper gauge was sunk into each of the two elevated runways leading to the reward tables (R1, R2), one containing a strong solution of oil of cloves, the other the solvent alone. Water contained in a dish hidden from sight was available on one of the reward tables; an empty dish was similarly located on the other. The right/left positioning of the crucible containing the oil of cloves and positive reward table were randomly interchanged.

FIGURE 1



Y-maze—schematic diagram showing spatial relationship of components.

Six thirst-motivated rats, which had previously been habituated to the apparatus by free exploration, were each given 30 trials a day in two sessions of 15 trials each. For three of these rats oil of cloves marked the runway leading to the positive reward table; for the other three it acted as negative stimulus. Each rat was placed on the start-table (S) and if choosing the correct pathway was allowed to drink for about 5 sec. before being returned to the start-table for the next trial. In instances where rats retraced their path an error was scored if the forepaws had previously crossed the position occupied by the negative crucible, but in practice use of this criterion was rarely necessary since rats, once started along a given pathway, almost invariably continued to reach the reward table.

During the first 300 trials the rats were allowed to retrace after error and to find their way to the correct table; for a further 300 trials the animals were immediately removed from the negative table and replaced on the start table for the next trial. At the end of these two series (600 trials per rat) no rat showed any evidence of learning, the correct and incorrect runways being chosen in approximately equal numbers. It seemed possible that remoteness of stimulus and reward might account for the rat's failure to learn and reversible one-way doors (D1, D2) were accordingly fitted on the immediate far side of the odour-containing crucibles. The door on the positive runway was arranged to swing outwards and so permit access to water on the reward table; that on the negative runway arrested further progress in a position where the rat could scarcely fail to detect the presence or absence of the olfactory stimulus. An additional 300 trials was run, any attempt to push against a door on the negative runway being scored as an error. There was no evidence of learning at the end of this period; nor did the administration of an electric shock as punishment for pushing the negative door prove effective during the course of a further 300 trials.

(*b*) *Rectangular choice box*

This apparatus consisted of an elevated runway leading to a choice box at the far end of which were hung two water bottles. The drinking spouts of these bottles were modified by the attachment of a short length of blind-ended tube just above the nozzle into which pledgets of cotton wool soaked in odorant or control solution could be placed. The spouts were insulated from the wire cage by rubber tubing, that containing the negative stimulus being connected to a source of potential about 45 V. above that of the floor of the cage. In drinking from this tube a rat would thus receive a shock derived from an estimated current of about 1 mA.

Six thirst-motivated rats were taught initially to run the length of the runway to reach a single central drinking spout. Later the single spout was replaced by the negative (odour charged) and positive (odour free) spouts whose relative positions to right and left of the choice box were varied in accordance with a Gellerman (1933) sequence. All six rats were run in randomized order for any one setting of positive and negative drinking tubes after which the tubes were reset for the next series of trials.

The behaviour of the rats in this experimental situation precluded the running of tests based on a fixed number of trials daily as had been used in the previous experiment. On receiving a shock as a result of choosing of the negative tube all rats refused to drink and during later tests, when motivation was raised, the rats' behaviour was characterised by the appearance of innately organized responses of the type seen in displacement reactions such as scratching, face-washing, leaping and hopping and, in several instances, attempted copulation by one male upon another placed in the choice box. These activities were interspersed with constant approaches and withdrawals to one or other of the drinking tubes. Where the tube finally sampled proved to be odour free (positive) the rats rapidly learned to drink from it in subsequent trials, all displacement activity disappearing. When, however, the positions of positive and negative tubes were interchanged all rats attempted to drink from the tube occuping the previously positive position rather than responding to the associated odour and, on receiving a shock, exhibited the identical range of behaviour seen during earlier training. Two of the six rats used, however, eventually learned to respond to the odour rather than to the position of the drinking bottles.

These observations suggested that the rat might satisfactorily be taught to perform olfactory discriminations by a method basically similar to that described provided that the time-consuming obstacles arising from (*a*) the initial fear of the apparatus and (*b*) the conflict between two incompatible orientating cues could be overcome. To this end, the apparatus described in the following section was devised in which the first of these difficulties was met by arranging for training to be carried out mechanically without requiring the presence of the operator and the second by eliminating as far as possible all guides to orientation other than could be derived from olfactory stimuli.

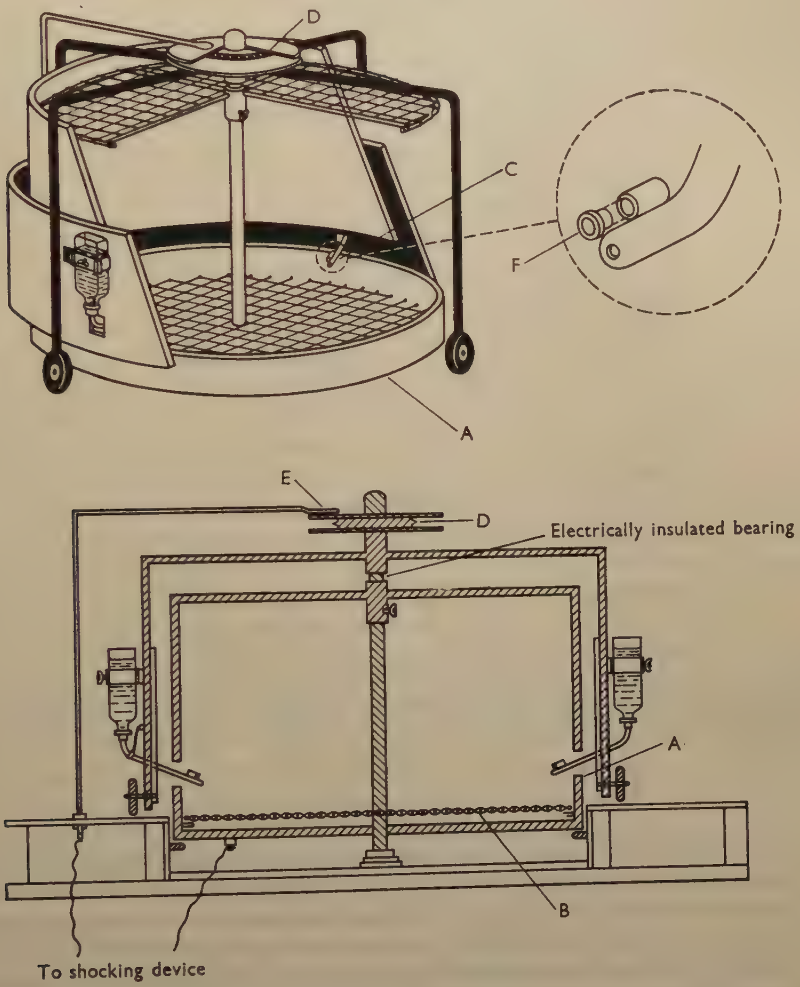
(*c*) *Circular choice apparatus*

The apparatus finally developed is illustrated in Figure 2 and consists essentially of two concentric sheet metal cylinders, the outer of which is free to rotate about the inner and is electrically insulated from it. The lower part of the inner cylinder consists of a circular tray (A) containing sawdust which is provided with a copper mesh grid (B) on which the rat stands. The upper part of this cylinder, suspended from a central pillar by a spider, is separated from the tray by a 1 in. gap through which the spouts of drinking bottles (C) attached to the outer cylinder protrude into the inner compartment. The roof of this compartment is closed with steel mesh, a door being provided to permit ready access. The outer cylinder is pivoted by means of an insulated bearing, about the central pillar and rides on rubber-tyred wheels. The spider supporting this component is surmounted by a sprocket and brass plate (D). The former enables the outer cylinder to be driven slowly around the inner by means of a chain drive from a similar sprocket fitted to the spindle of a kymograph. A copper foil brush (E) rides on the brass plate and this and the inner cylinder (and hence the copper mesh floor) are connected to the opposite poles of an electrical shocking device. The drinking tubes are similar to those described for the previous apparatus except that the impregnated cotton wool pledgets are carried in a detachable nylon capsule (F). The negative tube is connected to the outer cylinder by means of a wire and clip invisible to a rat inside the apparatus.

Preliminary training is carried out by fitting each drinking tube with a capsule containing the test odorant or control solution and connecting up the electric circuit appropriately. One or two thirsty rats are placed in the apparatus which is set to rotate at about 1 revolution in 12 hr. Only cues arising from the odour of the tubes are available to the rat, for the positions of the tubes relative to the living compartment and to the room in which the apparatus is housed are being constantly changed and the possibility of visual cues is reduced by keeping the apparatus in darkness. Later training is carried out manually, the rat being introduced into the apparatus for each trial and the positions of the drinking spouts set at random by rotating the outer cylinder between individual trials. The rat's success or otherwise is indicated by means of a trigger unit linked to the shocking system which illuminates a neon bulb each time the rat makes an error. Successes are scored for a constant and readily detectable concentration of the odorant until a plateau is reached when the animal is regarded as ready for determination of the olfactory threshold for this substance.

The ease with which rats could be trained in this apparatus fully justified its design. Rats left in the apparatus for two nights were usually fully habituated to the experimental situation and, after 24 hr. without water, would, without further training, attain scores significantly better than chance in scored blocks of manually conducted trials using strong concentrations of the odour (e.g. oil of cloves). Performance improved as a result of continued trials but 20 trials daily over 3 days was usually sufficient to ensure that only an occasional error was made although rats continued to improve their performance on weaker concentrations over a somewhat longer period.

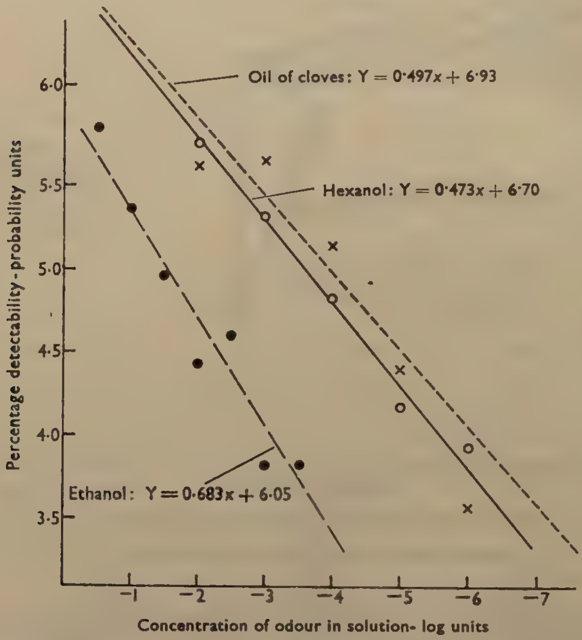
FIGURE 2



Circular choice apparatus—for description see text.

Figure 3 illustrates the decay in detectability with decreasing concentrations of oil of cloves (based on seven rats), hexanol (seven rats) and ethanol (six rats). The calculated probit regression lines show a very satisfactory fit to the data, and give median threshold values, i.e. the concentrations at which the rat may be expected to respond correctly over 50 per cent. of trials after making allowance for correct responses attributable to chance solution (see Finney, 1952) of 2·9 parts in 100 ml. for ethanol and of 1·7 and 1·3 parts in 100 ml. for hexanol and eugenol respectively.

FIGURE 3



Probit regressions based on the detectability of decreasing concentrations (log to base 10) of ethanol (● and — — —), hexanol (○ and ———) and oil of cloves (× and - - -).

Discussion

It is clear from the observations reported in this paper that the ease with which similar olfactory discriminations can be learned depends to a large extent upon the mode of presentation of the problem. A dominant factor in determining the likelihood of success would seem to be the degree of contiguity of stimulus and reward. Where these were remote, as in the Y-maze, learning did not occur whereas where the odour was directly attached to the drinking spouts, little difficulty was experienced.

The need for such immediate contiguity, which would not seem to be so essential for learning based on stimuli provided by other modalities of sensation, e.g. visual (Lashley, 1930), auditory (Pennington, 1938), provides a satisfactory means of explaining why some earlier workers, but not others, experienced difficulty in establishing olfactory discriminations. Thus in instances where rapid learning has been reported the positive stimulus has either been provided by the odour of the reward itself (Liggett, 1928; Lashley and Sperry, 1943) or, as in the present experiments, applied in close juxtaposition (e.g. French, 1940; Le Magnen and Rapaport, 1951;

Gruch, 1957). In this connection, the experiments of Swann (1933), who taught rats to burrow through piles of scented sawdust to reach food, suggest that the discrimination can fairly readily (though less readily than in the experience of the workers previously cited) be made at some distance from the reward provided that continuity of stimulus be maintained between the site of stimulus and the reward. On the other hand, in experiments where stimulus and reward have been more widely separated it has proved either difficult or impossible to establish an association between the two. Swann (1933), for example, was unable to teach rats to discriminate odours using a modified Lashley jumping stand while Liggett (1928) was no more successful with a T-maze or a Yerkes discrimination apparatus, except when the test odour used was a trigeminal irritant. The findings of Brown and Ghiselli (1938) who, by applying deterrent and reward in a manner similar to that used in the present experiment with the Y-maze, did succeed in training rats to avoid a pathway identified with the odour of creosote in about 750 trials, suggest that rats trained on the Y-maze might have learned the problem had the phase of training involving the use of electrically-charged doors been pursued further. There is doubt, however, whether creosote may be regarded as stimulating purely olfactory mechanisms (see Allen, 1937) and in any case the number of trials required for training would make the use of this method for determining olfactory thresholds on a statistical basis extremely laborious.

The experimental observations further suggest that, in the rat, the olfactory stimulus plays a relatively small part in orientation, for it is apparent from the behaviour seen in the rectangular choice apparatus after interchange of the positions of the positive and negative drinking tubes, that the animals tend to respond primarily to non-olfactory (presumably visual) cues. When steps are taken to minimize the influence of such cues, either in a rectangular choice box (Eayrs—in preparation) or in the circular choice apparatus already described, rats will more readily react to the olfactory component of the situation. Such observations are consistent with the inability of rats to follow an odorous trial (Liggett, 1928) and of the relatively unimportant part played by olfaction in maze learning by normal, but not by blinded, rats (Honzik, 1936; Casper, 1933).

The technique ultimately developed provides a useful instrument for the study of olfactory acuity and avoids most of the disadvantages, outlined in the Introduction, of methods previously used to study olfaction in animals. Thus training is rapidly and economically accomplished, and the conditions of the experiment can be well controlled. By using water as reward and electric shock as deterrent, and by randomizing the positioning of the odour in relation to drinking tubes and of drinking tubes in relation to other environmental features, the possibility of rats responding to stimuli other than those under test is reduced to minimal proportions. One disadvantage of the apparatus as at present constructed is that, from the point of view of determining olfactory thresholds, the concentrations of odorant molecules reaching the olfactory epithelium must be computed from factors such as their concentration in solution and their rate of diffusion. Only minor modifications are required, however, to enable a more direct measurement to be made by means of air-dilution of the odorant test-substance.

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STUDIES IN OLFACTORY ACUITY. II.

Relative Detectability of *n*-Aliphatic Alcohols by the Rat

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The ability of albino and black rats to detect *n*-aliphatic alcohols in the vapour phase has been investigated and probit analysis used to evaluate the results. At median threshold (= 50 per cent. success level) detectability tends to increase by logarithmic increments as the number of carbon atoms in the molecule is increased. However, a similar but reverse relationship occurs between carbon chain length and the gradient of the probit regression lines; and detectability at the 85 per cent. success level, as estimated by interpolation, shows a trend towards oscillation. It is suggested that this finding can resolve the apparent conflict in the literature concerning the pattern of odour intensity in homologous series, and that it may reflect the influence of low water solubility in limiting response to high concentrations of longer chain alcohols.

When expressed as pressures, median threshold values for alcohols in the rat vary directly with saturated vapour pressures; when expressed as thermodynamic activities intermediate and longer chain alcohols appear to be equally stimulating, whilst short chain alcohols show decreasing activities as the series is ascended. In several of the relations considered the position of methanol and dodecanol appears anomalous.

Introduction

Attempts to elucidate the nature of the olfactory process have resulted in an increasing number of studies in which relations between olfactory stimulating efficiency and physico-chemical properties in series of homologous compounds have been considered. In such series chemical and structural differences between successive members are at a minimum, whilst many physical properties alter progressively as the series is ascended. Conditions thus tend to favour an attempt to determine the particular physical properties of a molecule which exert greatest control over its olfactory stimulating efficiency. However, not only is much of the evidence resulting from this approach conflicting, but in many studies statistical design and treatment are inadequate. A further problem is that threshold data relating to species other than man or insects are scarce. The present study, in which the responses of rats to the series of *n*-aliphatic were investigated, was designed to provide further information on these points.

Material and Methods

Apparatus

The circular choice apparatus described in a preceding paper (Eayrs and Moulton, 1960) was used. Throughout these experiments the test odours and control solutions were contained in expendable nylon capsules which were discarded after each trial and replaced by a newly made-up set. The mode of conduct and scoring of the tests was as already described.

Animals

Young rats taken from two stocks initially derived by crossing black and white albino strains of the Norway rat (*Rattus norvegicus*, Berkenhout) were used. Since it has been claimed that olfactory acuity is influenced by the ovarian cycle (Elsberg, Brewer and Levy, 1935; Le Magnen, 1950; Schnedier and Wolff, 1955), only males were tested.

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Odorants

The *n*-aliphatic alcohols used, ranging in homologous series from methanol to dodecanol, were supplied by British Drug Houses Ltd., and were redistilled before testing. These, except for a small preliminary group of tests involving the lower members of the series in which distilled water was used as solvent, were first dissolved in 10 per cent. aqueous propylene glycol and subsequently diluted volumetrically with distilled water by successive factors of 10. The 10 per cent. propylene glycol solution used as solvent was similarly diluted to provide a control for the test substance.

Treatment of data

The percentage of correct choices made at each concentration were subjected to probit analysis to determine the median threshold response for each alcohol. The fiducial limits of estimates so derived are not altogether reliable (for discussion see Cheesman and Mayne, 1953) and have accordingly not been used in assessing the results.

Initially concentrations of alcohols eliciting the median threshold response were determined as molar values in solution, but the concentration of the alcohol vapour is clearly a more meaningful unit. In order to estimate this value it is first necessary to know the partial pressure (pt) of the alcohol vapour above the solution. This has been derived from the relation: $pt = ps \times M$, where ps is the saturated vapour pressure of the pure alcohol, and M is the mole fraction (i.e. the proportion of the total molecules of the solution which are alcohol molecules). The quantity ps has been calculated for the temperature of the experiment from tables compiled by Driesbach (1952).

The molar concentration (C) of the alcohol vapour can now be determined by substituting a value for pt and t (the temperature of the experiment), in the equation:

$$C = pt/(22{\cdot}41 \times \frac{t + 273}{273} \times 760) \text{ (cf. Ferguson and Pirie, 1948).}$$

Thermodynamic activities have been obtained from the relationship pt/ps which is the present instance gives a value numerically identical to the mole fraction (cf. Ferguson, 1951).

RESULTS

Results from a preliminary series of experiments in which 3 to 6 brown and albino rats were used are given in Table I. In the case of ethanol, median threshold values were determined using both water and propylene glycol as solvent, and since these values are closely similar they cannot be taken as supporting the view that the choice of solvent influences threshold. It is also clear that detectability tends to increase as the series is ascended. However, since variance at median threshold was high, a second series of trials was undertaken, using a larger number of subjects. This series, in which 27 to 29 black and albino rats were tested on each alcohol, was conducted in two stages: (i) ethanol, butanol, hexanol, octanol, decanol, and

TABLE I

DETECTABILITY OF *n*-ALIPHATIC ALCOHOLS IN THE VAPOUR PHASE BY THE RAT. PRELIMINARY SERIES

Alcohol	*Number of presentations*	*Slope of regression line*	*Log molar concentration of solution*	*Log molar concentration of vapour*
Ethanol* ..	864	0·694	−0·343	−4·649
Ethanol ..	576	0·323	−0·507	−4·213
Propanol* ..	864	0·300	−1·324	−5·989
Butanol* ..	864	0·454	−3·052	−7·222
Pentanol ..	864	0·223	−4·269	−9·262
Heptanol ..	384	0·234	−2·031	−8·828
Decanol ..	576	0·289	−4·943	−12·110

* Water used as solvent.

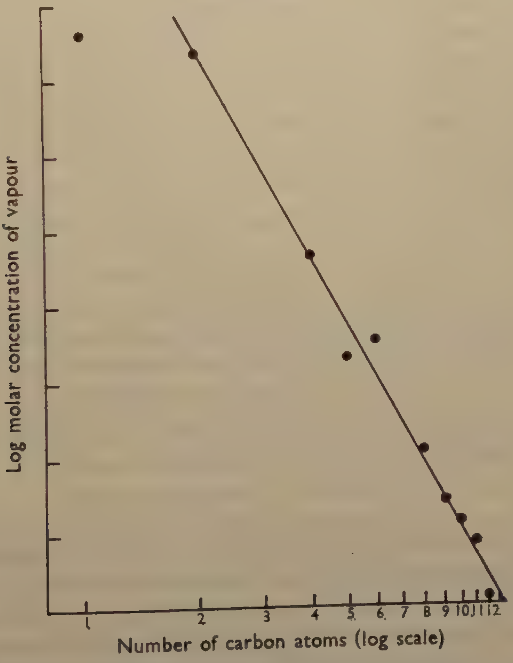
TABLE II

DETECTABILITY OF *n*-ALIPHATIC ALCOHOLS IN THE VAPOUR PHASE BY THE RAT. SECOND SERIES

Alcohol	*Number of presentations*	*Slope of regression line*	*Log molar concentration of solution*	*Log molar concentration of vapour*	*Log activity*
Methanol . .	1512	0·547	−0·9726	−4·4377	−2·1192
Ethanol . .	1624	0·564	−0·9292	−4·6453	−2·0654
Propanol . .	Interpolated from Table I			−5·9890	—
Butanol . .	1624	0·595	−2·7757	−7·3359	−3·9105
Pentanol . .	1512	0·374	−3·2624	−8·6647	−4·3971
Hexanol . .	1624	0·286	−3·0473	−8·4216	−4·1720
Heptanol . .	Interpolated from Table I			−8·8280	—
Octanol . .	1512	0·276	−3·6304	−9·9158	−4·7652
Nonanol . .	1512	0·293	−3·8383	−10·5763	−4·9731
Decanol . .	1512	0·264	−3·8097	−10·8729	−4·9442
Undecanol . .	1512	0·250	−3·7474	−11·1455	−4·8821
Dodecanol . .	1624	0·385	−4·2576	−11·8952	−5·3923

dodecanol; (ii) methanol, pentanol, nonanol, and undecanol using propylene glycol as solvent in each case. The results are given in Table II, in which the molar concentrations for propanol and heptanol, which were tested only in the first series of experiments, have been interpolated in the interest of continuity.

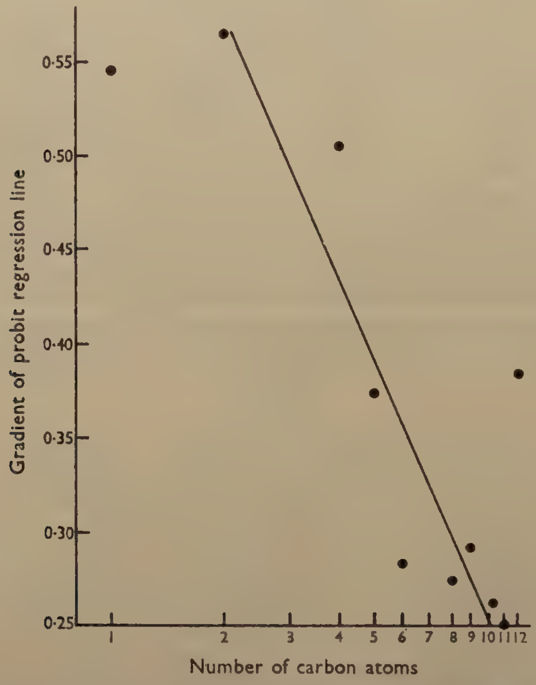
FIGURE 1



Relation of median threshold concentration of homologous series of alcohols, expressed as log molar concentration of vapour, to the number of carbon atoms in the chain. The aberrant value for methanol (one carbon atom) has been excluded from the computation of the regression (see text).

The most striking feature of these results is the tendency for odour intensity to increase by logarithmic increments as the series is ascended. This is shown more clearly in Figure 1, where molar concentrations of alcohol vapour at median threshold are plotted against the number of carbon atoms in the molecule. A linear and logarithmic relation also appears between the slope of the probit regression line and carbon chain length (Fig. 2), indicating that as the series is ascended there is a progressive reduction in the amount by which the response increases with each unit change in concentration. For reasons discussed below methanol has been excluded in computing the regressions of chain length on molar concentration and on slope (Figs. 1 and 2). In Figure 2 the position of dodecanol is clearly aberrant in comparison with the remaining members of the series and for this reason it also has been excluded from the computation of the regression line.

FIGURE 2



Relation of slope of probit regression lines for the detectability of alcohols forming a homologous series to the number of carbon atoms in the chain. The aberrant values for methanol and dodecanol have been excluded from the computations (see discussion).

One implication of these findings is that the pattern of detectability found is dependent on the criterion of response chosen. This is immediately apparent if the relative stimulating efficiency of the alcohols at the 50 per cent. success level is compared with the pattern derived, by substitution in the probit regression equations from the 85 per cent. success level (Figs. 1 and 2). At these higher concentrations there is a clear trend towards oscillation in response, alcohols with 4 to 11 carbon atoms occupying a concentration range of 2·3 log units as compared with 3·8 log units at the 50 per cent. success level. This trend continues until response to undiluted alcohols is being estimated.

Discussion

Odour intensity in homologous series

Among those who have also reported that the detectability of alcohols increases as the series is ascended are Cook (1926), Dethier and Yost (1952), and Hughes (1957), using flies, and Passy (1892), Skramlik (1948) and Kruger, Feldzamen and Miles (1955) in man. (However, the claims of the last workers refer only to the longer chain alcohols and only after corrections for vapour pressure are applied.) A similar relation to chain length is seen in human olfactory thresholds for alkyl mercaptans and in the amplitudes of the slow potentials evoked by ketones and aldehydes in the olfactory mucosa of the frog (Allison and Katz, 1919; Ottoson, 1958).

In the present study, in data given by Passy (1892) and in the responses of blowflies to alcohols, aldehydes and fatty acids (Dethier and Yost, 1952; Dethier, 1954*b*; Hughes, 1957) this relationship is clearly logarithmic. There is also some evidence from work on the dog (Ashton, Eayrs and Moulton, 1957), which has since been repeated, that the increasing detectability of fatty acids as the series is ascended is influenced by some factor which likewise alters logarithmically in value. Thus the generalization that, in several series, odour intensity rises as chain length expands has considerable support. It also accords with the action of certain of these series on a number of other biological systems. For example, the efficiency of alcohols in accelerating haemolysis (Ponder and Hyman, 1939), in producing a variety of narcotic effects (see Brink and Posternack, 1948), in stimulating the tarsal chemoreceptors of blowflies and the taste receptors of man (Dethier and Chadwick, 1947; see Dethier, 1956) increases by logarithmic increments as chain length is increased.

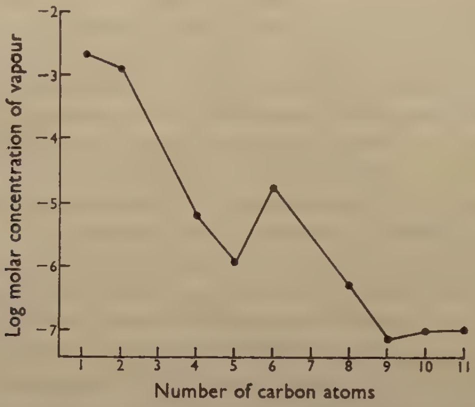
In contrast, however, the olfactory response to the homologous series of the fatty acids show one or more oscillations in detectability as the series is ascended—the first peak of stimulating efficiency being related to members with 3 to 5 carbon atoms, e.g. the studies of Passy (1893), Backman (1917*a*) and Skramlik (1948) in man, Neuhaus (1953) on the dog, Ottoson (1958) on the frog, and Schwarz (1955) on the honey bee. A similar oscillation has been found in an alcohol, a paraffin and a chloroparaffin series (Mullins, 1955*a*) and Ottoson (1958) reports that in an alcohol series the peak of maximum activity is related to the members with 7 to 8 carbon atoms.

It thus appears that there exist two strongly conflicting sets of data concerning the relationship between intensity of odour and position in a homologous series; and although differences in the species and techniques used by various workers doubtless complicate the problem they seem unlikely to offer a complete solution since different patterns have been reported in the same species (e.g. Mullins, 1955*a*, Passy, 1892) and by the same worker (Ottoson, 1958). In the following paragraphs, therefore, an attempt is made to reconcile these data in the light of the current findings.

Significance of relationship between intensity of response and concentration of vapour

(*a*) *As a means of reconciling divergences of evidence concerning the pattern of response.* The conclusion drawn from a comparison of Figures 1 and 2 that the pattern of detectability may vary with the criterion of response chosen offers a possible explanation of how these conflicting claims have arisen. Thus the lower the success score that is chosen to represent threshold, the greater the probability that a linear relationship between stimulating efficiency and chain length will be found. However, if it is assumed that similar concentrations of alcohol vapours above the olfactory organ of different subjects tend to produce similar patterns of response, variations in olfactory sensitivity between species could also have importance. For example, a criterion for success in the region of 85 per cent. is required to reveal an oscillatory pattern in the responses of rats to alcohols (Fig. 3), whereas in man Mullins (1955*a*) found an oscillation in detectability using what is clearly a much lower success value (i.e. the level at which subjects "found difficulty in recognizing every stimulus"). The present results suggest that the concentration of alcohol vapour required to elicit a low success level in man would elicit a much higher success level in rats, and thus, if the assumption holds that similar concentrations yield similar patterns of response, an explanation of such apparent anomalies is available.

FIGURE 3



Relation of alcohol concentration, corresponding to a 85 per cent. criterion of success, to the number of carbon atoms in the molecule. Concentrations were estimated by substitution in the equation for the probit regression for each alcohol.

Doubtless differences in techniques, methods of analysis, purity of test compounds, amount of mucus in the nasal cavity and similar variables may also contribute to the complexity of the picture. Kruger, Feldzamen and Miles (1955), for example, were unable to find any change in the pattern of intensity over "a wide range of dilutions" of alcohols (molar concentrations were not specified). But these workers were using a subjective iso-intensity odour scale and it is difficult to know what relation this criterion of response bears to that used by other workers.

However, the possible cause of this variation in response pattern merits consideration since it throws light on certain aspects of the olfactory process.

(*b*) *As a possible cause of the transformation of the pattern of response.* Oscillation in biological activity within an homologous series of compounds is generally considered to be the result of interaction between two opposing factors, the first tending to cause an increase in activity as the series is ascended, and the second having the opposite effect. According to Sexton (1953), a common explanation of the second phase is that at a certain point in the series the concentration of a compound needed to produce a given effect exceeds its water solubility. At this stage the addition of further quantities of the compound will not increase activity.

There are grounds for believing that an effect of this kind could largely account for the pattern of response seen in Figure 3. Thus the progressively increasing detectability of the short chain alcohols is associated with complete miscibility in water, whilst in the longer chain alcohols the decay in stimulating efficiency corresponds with diminishing water solubility. If this explanation is correct the transformation of response pattern from the oscillating to the linear form (cf. Figs. 1 and 3) could be related to the declining importance of water solubility as a limiting factor and thus to the emergence of whatever property controls activity in the short chain alcohols as the dominant activity throughout the series. The logarithmic relation between chain length and slope in alcohols of limited solubility accords with this view since water solubility also decreases by logarithmic increments as chain length is increased.

However, response increments for alcohols of 5 to 12 carbon atoms not only fail to continue their decline at high concentrations, but show a marked increase in magnitude. Thus if the theory is correct it is necessary to postulate the intervention of a further factor reinforcing response at high concentrations.

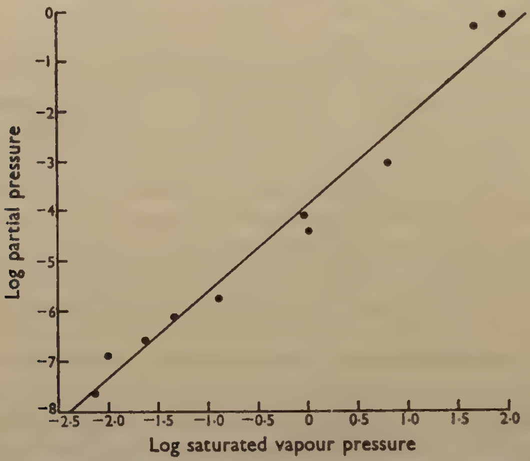
In the case of the apparently similar effect which occurs in the responses of the honey bee to the vapours of acetic acid and phenol Jones (1952) has suggested that at high concentrations the vapours act only as irritants whereas at low concentrations the olfactory sense alone is effective. But although all objective evidence available supports the view that in both insects and mammals irritants irritate only in high concentrations (see Parker and Stabler, 1913; Dethier, 1953; Neuhaus, 1953), it is premature to consider whether the present anomalies are due to the intervention to trigeminal response or to some other factor such as direct chemical action or the excitation of different types of olfactory or other receptors. It is clear that much more work will be required to elucidate the nature of these effects.

Implications for an understanding of the nature of the olfactory process

If, as seems highly probable, the olfactory hairs or corpuscles (cf. Hopkins, 1926; Clark, 1957) are covered by a thin film of mucus or adsorbed moisture, reduced water solubility may restrict the stimulating efficiency of the alcohols by limiting their access to the receptor surface and may in this way be responsible for the oscillatory pattern of detectability. If this were so such a pattern could hardly give a true indication of the basic sensitivity of the receptors to alcohols. But in any case the pattern of increase in response to alcohols as the series is ascended (Fig. 1) seems here more likely to provide insight into the nature of the olfactory process since at median threshold anomalies of the type occurring at higher and lower levels of success have less influence. At this level the odour intensity of the alcohols is clearly determined by some property which tends to alter by logarithmic increments as chain length is increased.

Ferguson (1939) and others have pointed out that several physical properties, including oil-water partition coefficients, surface activity and vapour pressure show a similar relationship to chain length within an homologous series. Thus when the median thresholds for alcohols given in Table I are expressed as pressures and plotted against their saturated vapour pressures (Fig. 4) the relation is clearly linear. This type of relation is characteristic of narcotic and toxic phenomena in which it is assumed that an equilibrium exists between the external phase and the internal biophase. Ferguson (1939) has argued that when such an equilibrium exists the thermodynamic activity of the test compound will have the same numerical value in all phases. Thus the activity of the substance at the site of biological action can be derived from a knowledge of its concentration outside the organism. Thermodynamic activity is defined as partial free molal energy referred to a standard state and is numerically equal to the relative saturation of the vapour of the compound (i.e. pt/ps, see Ferguson and Pirie, 1948). (For a fuller discussion of the rationale behind the application of analysis in terms of thermodynamic activities, see Ferguson (1939, 1951), Ferguson and Pirie (1948), Brink and Posternack (1948) and Dethier (1954*a*).) Applying this form of analysis to data on the olfactory responses of blowflies, Dethier and Yost (1952) and Dethier (1954*b*) found that thresholds for *n*-aliphatic alcohols and aldehydes of intermediate chain length were approximately equally stimulating and they therefore concluded that in these series olfaction may involve an equilibrium process. Similarly Ottoson (1958), in a study of the slow potentials evoked in the olfactory mucosa of the frog, has reported that alcohols of intermediate chain length stimulate at equal thermodynamic activities.

FIGURE 4



Relation of median threshold, expressed as partial vapour pressure, to saturated vapour pressure.

It seems pertinent therefore to examine the pattern of median threshold values, reported above, in terms of activity units (Table I). In Figure 5 these activities are plotted against chain length and the resulting pattern suggests that, although they show an overall tendency to decrease with increasing chain length, the alcohols tested (with the exception of methanol and dodecanol) tend to fall into two groups:

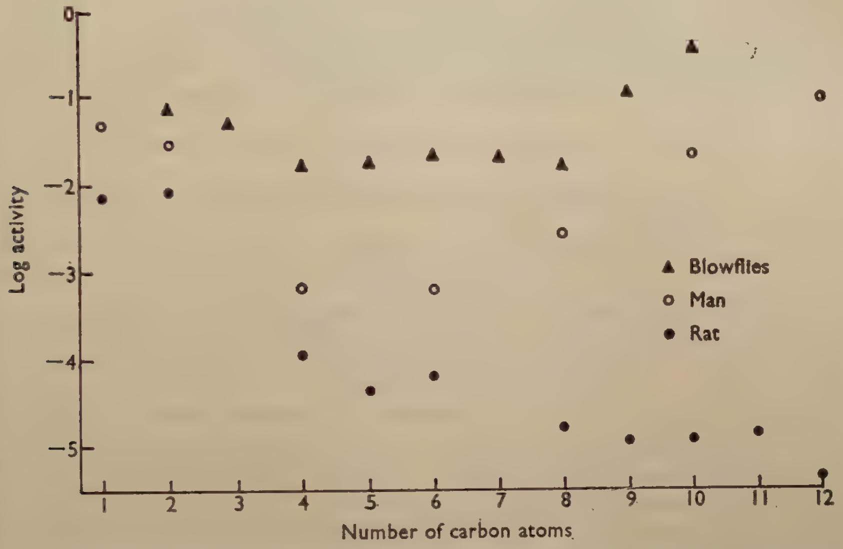
(1) Members with 2 to 4 carbon atoms which are detected at decreasing activities as the series is ascended.

(2) Members with 5 to 11 carbon atoms which are approximately equally stimulating.

If the behaviour of the longer chain alcohols is excluded such a conclusion is essentially in agreement with the findings of Dethier and Yost (1952), Dethier (1954*b*) and Ottoson (1958) whilst an analysis of data given by Ashton, Eayrs and Moulton (1957) suggests a similar division in a fatty acid series. However, although the trend shown by the lower alcohols accords with all available evidence some studies show a different pattern in remaining members. Thus, according to an analysis made by Dethier (1954*a*) of scattered data on olfactory response for man and for flies (Cook, 1926) in a number of homologous series, a decrease in activities occurs as the series is ascended. Further, the oscillation which Mullins (1955*a*) reports in odour intensity in three series, is also shown when thresholds are expressed as activities (Mullins, 1955*b*; see also Fig. 5) and a similar pattern appears in more meagre data on human olfactory thresholds for alcohols (Gavaudan, Brebion, Poussel and Shutzenberger, 1948).

Further information is clearly needed, but it may be tentatively concluded that whilst olfaction in the rat for medium and long chain alcohols may involve an equilibrium process, olfaction for shorter chain alcohols may not. Ottoson (1958) has suggested that solubility properties may account for a similar break which he reports in this series.

FIGURE 5



Relation of median threshold concentrations, expressed as thermodynamic activities, to chain length in a series of *n*-aliphatic alcohols. Olfactory responses of rats are compared with those of blowflies (Dethier and Yost, 1952), and man (Mullins, 1955*b*).

A further indication of the complexity of factors which may influence the detectability of alcohol vapour is seen in the frequent failure of methanol and dodecanol to conform to the trends shown by the remaining alcohols (Figs. 1, 2 and 5). Other workers have noted, or their data suggest, the greater stimulating efficiency of methanol than its position in the series would seem to warrant (Passy, 1892; Dethier and Yost, 1952) and such anomalies are also a feature of toxicity data (see Passy, 1892; Ostergren, 1944; Ferguson and Pirie, 1948). The aberrant behaviour of the high alcohols in their narcotic effects has been noted by Brink and Posternack (1948).

The present study tends to support the suggestions of Beckman (1917*b*), Ottoson (1958) and others that the solubility characteristics of compounds may play an important part in determining their olfactory stimulating efficiency, and indicates that the mechanisms of olfaction may not differ greatly in the rat, in the frog (Ottoson, 1958), and in blowflies (Dethier and Yost, 1952). Finally, the similarity between the present findings and those of Ottoson (1958) suggests that olfactory data obtained by behavioural techniques can closely reflect the patterns of comparable data obtained by use of electrophysiological methods.

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SHORTER ARTICLES AND NOTES

TWO MORE VISUAL THEOREMS

BY

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The basis of the widely held opinion that the spectral sensitivities of the mechanisms determining trichromacy must be linearly related to the spectral mixture functions is examined, and a proof from simple assumptions is stated.

It is proved also that, on the van der Velden hypothesis of independent sensitive units, a spatial or temporal summation law of the form $AI^n = c$ implies a frequency-of-seeing curve of the form $Q = 1 - e^{-KI^n}$ (Q = probability of detecting a stimulus of size A and intensity I; n, c and K are constants).

Introduction

This theoretical paper is a sequel to one already published in this *Journal* (Brindley, 1957), and presents and proves two more theorems with applications in visual physiology and psychology. These are numbered 3 and 4, following the two of the former paper.

Theorem 3 is of respectable antiquity. First propounded and used by König and Dieterici (1886), it seems to have been regarded by them as self-evident, and I cannot discover that any subsequent writer has published a proof of it, though many have accepted and used it. The chief value of now devising a proof is that the assumptions which underlie its general acceptance are thereby clarified, and we are the better able to judge whether in given circumstances it is likely to be exactly true, approximately true, or altogether false.

Theorem 4 is new. Its application is to the testing of the extent of validity of the important hypothesis, first clearly set out by van der Velden (1944), that the spatial or temporal segments of a large or long visual stimulus are detected *independently* by the retina and visual pathway. This application is made in detail elsewhere (Brindley, 1960, Chapter 6).

Definition

The reciprocal of the amount of light of wavelength λ required to produce a given constant response in a mechanism is called the *spectral sensitivity* of that mechanism for the wavelength λ. The "amount" must be measured in units which remain meaningful despite a change of wavelength; customarily, units either of energy or of number of quanta (per second per steradian, etc.) are used, the former being experimentally more direct, the latter better for correlation with photochemical properties.

If the substitution postulate holds for a mechanism, then its spectral sensitivity will be invariant (except for a factor independent of wavelength) when the response-criterion at which it is measured is changed. This invariance, however, is no essential part of the concept of a spectral sensitivity.

Statement of the Theorems

Theorem 3

In trichromatic vision, the spectral sensitivities of the three mechanisms determining the trichromacy must be linear functions, with coefficients independent of test wavelength, of the amounts of any three specified primaries required to match a constant amount of a test light of variable wavelength.

Theorem 4

If the relation between the intensity (I) and temporal or spatial size (A) of a visual stimulus required to attain a constant probability of seeing is of the form $AI^n = c$, where n and c are constants, and if, over the range of sizes considered, all stimuli are divisible, temporally or spatially, into a large number of similar constituents the detection of which is independent, then at any given size of stimulus the probability of seeing (Q) must be related to the intensity by $Q = 1-e^{-KI^n}$, where K is a positive constant.

Assumptions Required in the Proof of Theorem 3

We shall assume the postulate of unidimensional response and the substitution postulate (Brindley, 1957). We shall also use Case 1 of Theorem 2. This does not constitute a further assumption, since it is deducible from the first two and the experimental law of uniqueness of colour matches.

Proof of Theorem 3

Let r_λ, g_λ, and b_λ be the amounts of the primaries, r, g and b required to match unit amount of light of wavelength λ. One of these amounts must be negative; we may suppose that it is b_λ.

Let ρ_r, ρ_g, ρ_b and ρ_λ be the spectral sensitivities of the red-sensitive mechanism to r, g, b and λ respectively, and let λ be such that $\rho_\lambda \neq 0$. Then this mechanism is affected to the same extent

by amount $\rho_r r_\lambda/\rho_\lambda$ of wavelength λ
as by amount r_λ of primary r (Subst. post.),

and by amount $\rho_g g_\lambda/\rho_\lambda$ of wavelength λ
as by amount g_λ of primary g (Subst. post.),

and by amount $\rho_b b_\lambda/\rho_\lambda$ of wavelength λ
as by amount b_λ of primary b (Subst. post.),

and by amounts r_λ of primary r plus g_λ of primary g as by amounts $-b_\lambda$ of primary b
plus 1 of wavelength λ (Case 1 of Theorem 2, since these match),

and therefore by amount $\rho_r r_\lambda/\rho_\lambda + \rho_g g_\lambda/\rho_\lambda$ of wavelength λ as by amount 1—
$p_b b_\lambda/\rho_\lambda$ of wavelength λ (Subst. post.).

Therefore $\rho_r r_\lambda/\rho_\lambda + \rho_g g_\lambda/\rho_\lambda = 1-\rho_\lambda b_b/\rho_\lambda$, for if they were not equal, application of the substitution postulate would prove $\rho_\lambda = 0$, contrary to the assumption made above.

Therefore $\rho_\lambda = \rho_r r_\lambda + \rho_g g_\lambda + \rho_b b_\lambda$.

The theorem is thus proved, since ρ_r, ρ_g and ρ_b are independent of λ.

This proof does not involve the concept of extra-spectral "fundamental stimuli" (Wright, 1934, and other writers), with which it is customary to introduce the spectral sensitivities of the mechanisms determining trichromacy. Proofs can be devised that start from "fundamental stimuli"; but those that I have been able to invent involve the same assumptions as are made above, and also others more difficult to justify.

Of the assumption needed for the proof, the law of uniqueness of colour matches is experimental, and the postulate of unidimensional response is necessarily involved in the concept of a spectral sensitivity. Only the substitution postulate remains to be doubted. Is Grassmann's third law sufficient evidence for its truth? Logically it is not; Grassmann's third law can be deduced from the substitution postulate (given Theorems 1 and 2), but not the converse. However, by scientific standards the argument from Grassmann's law to the substitution postulate is a good one; the substitution postulate is equivalent to a fairly small extrapolation from the verifiable instances of the law, and its credibility is enhanced by its being implied by the hypothesis that the three mechanisms determining trichromacy are receptive pigments, for which there is much independent evidence (see Brindley, 1960, Chapter 7).

Proof of Theorem 4

If the number of independently detected constituents of a stimulus is sufficiently large, boundaries can be neglected, and the number be assumed proportional to the size.

Let the number of independently detected constituents in a stimulus of size A be rA, let the probability of detection of each one of them be P, and let the probability of detection of the whole stimulus be Q.

Then $1 - Q = (1 - P)^{rA}$,

therefore $\ln(1 - Q) = rA \ln(1 - P)$.

Let Q_o be the value of Q for which the law $AI^n = c$ has been experimentally established.

$$\begin{aligned}\text{Then } \ln(1 - Q_o) &= (rc/I^n)\ln(1 - P)\\ &= (c/AI^n)\ln(1 - Q),\\ \text{therefore } \ln(1 - Q) &= (A/c)\ln(1 - Q_o).I^n\\ &= -(A/c)\ln\frac{1}{1 - Q_o}.I^n\end{aligned}$$

Therefore $Q = 1 - e^{-KI^n}$, where K is the positive constant $(A/c)\ln\dfrac{1}{1 - Q_o}$

The frequency-of-seeing curve (i.e. the curve of Q plotted against $\log I$) is thus determined by the empirically known law of spatial (or temporal) summation and the hypothesis that the detection of constituents is independent. The *shape* of the curve is independent also of the size of stimulus with which it is tested (provided that this is within the range over which $AI^n = c$), and of the probability-criterion Q_o at which $AI^n = c$ was established, for varying A or Q_o merely shifts the curve along the axis of $\log I$.

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A NOTE ON SOME UNUSUAL HANDEDNESS PATTERNS*

BY

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It is widely held that the "ambidextrous" individual is almost always a natively left-handed person, trained to use the right hand but still naturally skilful with the left (Wile, 1934; Brain, 1945; Burt, 1950). Whatever the truth of this view, it is at all events clear that left-handed individuals who have been obliged to write with the right hand commonly show a greater variety of hand preferences than similar individuals who have been permitted to write with the left (Hildreth, 1949; Humphrey, 1951). At the same time, it is noteworthy that right-hand preference for certain tasks is not uncommon even among sinistrals who have been allowed—or even encouraged—to persist in their left-handed writing (Humphrey, 1951). For instance, no fewer than ten of the 35 left-handed writers studied by Humphrey (1951) were stated to prefer the right hand for throwing, for unimanual games, or for both these activities. It is evident, therefore, that enforced shifting to the use of the right hand in writing cannot be the sole cause of "mixed" hand preference. In some cases, at least, a somewhat different explanation of "ambidexterity" must be sought.

In an enquiry modelled upon that of Humphrey (1951), ten subjects have been found who are left-handed writers but preferentially right-handed for a variety of of other activities. These represent roughly 15 per cent. of the total group of left-handed subjects so far studied. Of the ten subjects, five consider themselves to be left-handed, four ambidextrous, and one described herself as "split" in her hand preferences. The object of this note is to give a short account of the lateral preference patterns in this atypical group.

Procedure and Subjects

The questionnaire devised by Humphrey (1951) was used in this study. It consists of 20 questions designed to assess hand preference in a number of skilled acts which are common to most educated people. No account is taken of possible differences in strength or skill as between the two hands. From the answers given, an approximate "sinistrality index" (S.I.) is calculated for each subject from the formula $(L + \frac{1}{2}E)/N$ where L and E refer to the number of questions answered "left" and "either" respectively and N is the total number of questions. An S.I. of 1·0 would thus indicate consistent left preference and an S.I. of 0·0 consistent right preference. An index of 0·5 indicates virtual "ambilaterality." We have also followed Humphrey's procedure in adopting an arbitrary "handedness classification" in terms of the preferred hand in writing, throwing and unimanual games such as tennis or squash. Thus L – R – R (which was the pattern displayed in most of our subjects) indicates a left-handed writer who prefers to throw a ball and use a tennis racket with his right hand.

The subjects, all of whom were young University graduates or undergraduates were asked some additional questions concerning ocular and foot preference and certain other matters presumed to bear on laterality, e.g. relative skill of the two hands, tendency to mirror writing, and proneness to confuse left and right. Information regarding familial handedness was also sought. Finally, the time taken by every subject to sign his name and write a short text to dictation with either hand was recorded.

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* Based on a short communication to the Experimental Psychology Society at a meeting held in Cambridge on 15th July, 1959.

Results

The principal findings are shown in Table I. It will be seen first, that the S.I.s are distinctly low, indicating an appreciable admixture of right hand preferences in all subjects. (Indeed, in the case of the first three subjects, writing and drawing are the only major skills for which the left hand is consistently preferred.) Secondly, the incidence of right foot and eye preference is distinctly high, six subjects being both right-footed and right-eyed and only one being both left-footed and left-eyed.

TABLE I

Lateral Preference Patterns in 10 Left-handed Writers

Subject	*Sex*	*Age*	*S.I.*	*Handedness classification*	*Foot preference*	*Eye preference*	*Familial sinistrality*
1. V.P.B.	F	21	0·15	L – R – R	E	R	Maternal grandmother; brother
2. C.D.M.	M	21	0·15	L – R – R	R	L	Maternal grandmother
3. A.B.	F	21	0·18	L – R – R	R	R	None ascertained
4. C.L.	F	24	0·35	L – R – R	L	L	Two first cousins
5. P.A.J.	M	23	0·38	L – R – R	? R	L	Maternal grandmother; mother; brother; nephew
6. G.W.	F	35	0·40	L – R – R	R	R	Paternal grandfather
7. J.W.A.	M	21	0·45	E – L – R	R	R	Mother
8. M.G.G.	M	20	0·53	L – R – R*	R	R	One maternal uncle
9. D.M.A.S.	M	21	0·58	L – R – R*	R	R	None ascertained
10. C.M.	M	22	0·65	L – R – R	R	R	None ascertained

S.I. denotes sinistrality index.

"Handedness classification" summarizes manual preference with regard to writing, throwing and unimanual games (Humphrey, 1951).

R* indicates right-handed for games, with the exception of table tennis.

E denotes lack of consistent unilateral preference.

Thirdly, there is evidence of familial sinistrality in seven cases, though in only two is a parent reported as left-handed. In three cases no evidence of familial sinistrality could be ascertained.

It is also of interest that three subjects (Nos. 1, 2 and 7) confessed to noteworthy lack of skill in either hand—suggestive of the classical "ambilaevous" condition first described by Galen—and two (Nos. 3 and 7) described some difficulty in discriminating right and left, especially when giving directions as to routes. Seven subjects had some facility in mirror writing.

On the *writing tests*, speed and quality of writing with the non-preferred (right) hand were, in general, but little inferior to performance with the preferred hand, testifying to appreciable ambidexterity. (In one case (No. 7) writing performance with the two hands was virtually identical, but this subject had practised writing with his non-preferred hand since the age of 11. No other subject reported having practised writing with the right hand.)

Discussion

These unusual preference patterns might be explained in various ways. First, it might be argued that some, at least, of our subjects were naturally right-handed, their left-hand writing being attributable to some incidental psychological perversity. In this connection, Scheidemann and Colyer (1931) have suggested that isolated left-handed writing in an otherwise right-handed child may derive simply from imitation, conscious or unconscious, of a left-handed parent, teacher or admired school fellow. In such cases, these authors claim, reversal of the writing hand is as a rule both easy and successful. As applied to our present cases, this interpretation might gain support from the relatively good writing performance of the subjects with the non-preferred hand, even in the absence of special practice. At the same time, no direct evidence was obtained which suggested that left-handed writing habits had in fact been acquired in this way. No subject was able to recall an early identification with a left-handed writer and should any such have occurred it must almost certainly have remained unconscious. There are also certain other considerations which militate against this explanation as generally applicable to the left-handed writer (cf. Burt, 1950).

A more plausible explanation might perhaps be given in terms of training and social convention. Thus it might be supposed that our subjects were natively left-handed and that their tendency to write with the left hand had been fostered by a permissive attitude at home and at school. At the same time, this permissiveness may not have extended in the same way to other types of unimanual activity normally carried out in a social context. For instance, almost all left-handed children come to adopt right-handed table manners and the urge to conform may likewise govern the adoption of right hand preferences in the use of tools and in certain games. None the less, it is difficult to see why social pressures of this kind should affect some left-handed writers so much more than others, though it is possible that considerations of temperament are involved to some extent (Blau, 1946). It is also possible that some left-handed people have undertaken a measure of self-training in the use of the right hand, perhaps in the belief that ambidexterity confers a real advantage upon its possessor. None the less, it might seem rather doubtful whether training and convention alone are sufficient to explain the high frequency of right hand preferences in the present group.

A third line of explanation—and one to which we ourselves incline—involves considerations of constitutional variability. Although handedness is commonly treated in terms of a simple dichotomy, there is good reason to believe that lateral dominance is in reality a graded characteristic and that constitutional differences exist in both the strength and the consistency of lateral preference. In our present cases, it might be supposed that the degree of inborn sinistrality was relatively weak, leading to a lack of clear unilateral hand preference and to certain inconsistencies in preference as between hand, foot and eye. As a result, one might expect hand usage to have evolved in almost random fashion, being determined to a far greater degree than is usual by incidental factors, either personal or environmental. For instance, one subject (No. 6) reported that she tended to prefer her right hand for activities involving muscular effort (e.g. throwing) and her left for activities requiring close guidance (e.g. sewing or billiards). Although most individuals tend to use the preferred hand irrespective of considerations of relative strength, it is possible that a dissociation of this kind is not uncommon among those who are poorly lateralized. Another subject (No. 1) remarked that she thought she had been more strongly left-handed as a child but had gradually become less so as she grew up. She could not recall any conscious wish or intention to shift her hand preference and quite certainly had not been subjected to pressure by others to do so. This might suggest delayed maturation of lateral dominance in a virtually ambilateral (and somewhat "ambilaevous") individual. One may also point out that some slight admixture of left-hand preferences is by no means uncommon among right-handed individuals with left-handedness in the family history. This can hardly be explained in terms of social training and is presumably due to an obscure genetical influence.

In the light of these considerations, we would suggest that atypical handedness patterns of the type described are only indirectly related to factors of training and social convention. We believe that a basic sinistral tendency, linked with some constitutional factor, was present in all ten subjects, but that this tendency was insufficiently marked to constrain strong and consistent unilateral preferences. In consequence, hand usage showed far greater variability than is usual and inconsistencies of preference were strongly marked. This finding may perhaps be related to recent neurological evidence suggesting that unilateral cerebral dominance is often far from clear-cut in individuals who are partly left-handed or who display mixed patterns of hand preference (Humphrey and Zangwill, 1952; Ettlinger, Jackson and Zangwill, 1956). At all event, it would appear to warrant reconsideration of the older concept of the "ambidexter" as a basic biological variant.

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THE EFFECT OF TEMPORAL SEPARATION AND PRIOR HABITUATION UPON PRECONDITIONING*

BY

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The effect of temporal separation and prior habituation was tested by measuring response transfer in a shuttle box following different initial treatments. Thirty hooded rats were split into three main groups and six sub-groups. One main group was preconditioned with concurrent light and sound stimuli, another with temporally spaced stimuli, and a control group had no preconditioning. Half of each main group was permitted to explore the apparatus before preconditioning on the supposition that this might reduce emotionality and hence reduce startle or attention responses.

It was found that concurrent stimulation produced significantly greater response transfer than in controls, whereas preconditioning with spaced stimuli did not. Prior habituation produced no significant effect on the amount of response transfer.

INTRODUCTION

This experiment was undertaken shortly after the appearance of Reid's (1952) criticism of Brogden (1939). In view of the theoretical importance attached to preconditioning by Birch and Bitterman (1949) it seemed to be of some urgency that the status of the phenomenon should be further examined. Was preconditioning a genuine conditioning phenomenon or did it arise from an inadequacy in Brogden's experimental design? If preconditioning were genuine it could be expected to bear some relationship to conventional conditioning parameters. As studies of classical conditioning (Wolfle, 1932, Razran, 1957) had shown that temporal separation of the CS and the UCS was an important variable, it was decided to examine the effect of temporal separation of the preconditioning stimuli. It should be noted that at the time of commencement of this experiment the results of Silver and Meyer (1954), which show the importance of temporal order of stimulation, were not available.

When Brogden (1939) introduced the term "sensory preconditioning" he did not cite the experiment of Narbutovitch and Podkopayev (cited by Konorski, 1948) which led to the supposition that paired stimuli could become associated on the basis of an orientation response. In a recent paper on the neurophysiology of conditioning Gastaut *et al.* (1957) have strengthened this view. In designing the present experiment the effect of prior habituation to the apparatus was tested in order to see whether this might reduce emotionality during preconditioning and, hence, startle or attention responses made to the preconditioning stimuli.

If either of the preconditioning stimuli acted as a CS for an orientation response to the other stimulus sufficient temporal separation could be predicted to annul the effect of preconditioning. As previous studies had shown that temporal separation of CS and UCS greater than 4 sec. made conditioning negligible, it was decided to separate the onset of the stimuli by an amount greater than this. Following Brogden's general procedure, after preconditioning its effect was assessed by conditioning the animal with one of the preconditioning stimuli (light) then the remaining stimulus (sound) was substituted in test trials. As the shuttle-box procedure seemed to offer a convenient method of conditioning the animals it was planned that, after preconditioning, an avoidance response would be conditioned using light as CS, and then sound would be substituted as CS in further training. Experimental groups preconditioned with or without temporal separation of stimuli during preconditioning could then be compared with each other, and with a control group lacking preconditioning, on the amount of transfer shown by comparing the percentage saving in number of responses required to attain the learning criterion using sound as CS with the number required using light as CS. It was predicted that when the stimuli were temporally concurrent during preconditioning most saving would occur, that the least saving would occur in the control group, and that the temporally spaced group would not differ significantly from the control group. With regard to prior habituation it was predicted that this would reduce the effect of preconditioning in the experimental groups and, in particular, in the concurrent group.

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* Based on a paper presented to the 13th Annual Conference of the British Psychological Society (Australian Branch), Sydney, August, 1957.

METHOD

Apparatus

A shuttle-box was used, of interior dimensions 24 in. long, 12 in. wide, 11 in. high, the floor of which consisted of two separately wired electrifiable grids, each 12 in. square. These were separated by a central hurdle 2 in. high, running across the width of the apparatus. A brief shock (0·25 Ma.) was applied alternately to each grid during training procedures. The top of the hurdle was constantly electrified during conditioning, but not during habituation and preconditioning. The light stimulus consisted of a 6 V. lamp centrally mounted, facing downward into the box. The sound stimulus consisted of a pure tone 1000 c.s. of 40 db. intensity (reference level 0·0002 dynes per sq. cm.) emanating from a loudspeaker mounted in the centre of one wall of the box facing into the box.

Timing relationships

During preconditioning, for the temporally concurrent group, light and sound stimuli of 2 sec. duration were regularly paired at 15 sec. intervals; for the temporally spaced group light and sound stimuli were presented individually, the onset of stimuli being spaced by 7·5 sec. During conditioning a 2 sec. CS was delivered with its cessation co-incident with the onset of the UCS (shock.)

Subjects. Thirty experimentally naïve hooded rats, 2 to 4 months old were used as subjects.

Procedure. After initial handling for 2 weeks, half of the subjects randomly selected, were allowed to explore the shuttle box for three 1-hr. periods on three successive days, the last period being on the day preceding preconditioning. Subjects were further divided into three main preconditioning treatments:

The *temporally concurrent* group was given 500 presentations of paired light and sound stimuli in one 125 min. period. The *temporally spaced* group was given 500 presentations of light and sound which, although delivered regularly, were at no time contiguous or concurrent. The control group was simply enclosed in the apparatus for 125 min. without experiencing the preconditioning stimuli. All animals were preconditioned individually.

Immediately following the above treatment the animal was trained to avoid shock, using the light as CS. The criterion was a total of 10 successful avoidance trials, i.e. jumping over the hurdle within 2 sec. following onset of the CS. In the final phase sound was immediately substituted for light as CS and the amount of transfer was estimated by training the animal to the same learning criterion as in the previous phase.

The procedure may be summarized by stating that the animals were first habituated as necessary, then preconditioned as necessary, then conditioned using light and, finally, conditioned using sound.

Results

The percentage saving scores obtained by this method are shown in Table I. A positive percentage saving resulted if the subject attained the learning criterion with sound as CS in less trials than with light as CS. Analysis of variance applied to this data revealed that the overall difference between groups was significant ($F = 4{\cdot}97$ with 2 and 24 d.f.) whereas the effect of prior habituation was not significant ($F<1$ with 1 and 24 d.f.). Application of the Fisher-Yates exact test (Finney, 1948) to the data revealed that whereas the concurrent group differed significantly from the controls ($p<0{\cdot}05$), the spaced group did not so differ ($p>0{\cdot}05$), furthermore, the two experimental groups differed significantly ($p<0{\cdot}05$).

TABLE I

Percentage Saving using Shuttle-Box Method*

	Concurrent group	*Spaced group*	*Control group*
Experienced Subjects†	+6·2	−9·5	−30·1
Naïve Subjects	+29·4	−6·6	−54·0

* Light was used first as CS and finally sound as CS. If less trials were needed to attain the learning criterion using sound the saving percentage was positive.

† *n* = 5 in each cell.

Discussion

These results appear to indicate that separating the onset of two preconditionng stimuli (light and sound) significantly reduces the effectiveness of preconditioning. At the same time, if preconditioning were due, as Reid (1952) suggested, merely to the fact that experimental subjects had more experience of the test stimulus than controls prior to the test phase, it is difficult to see why subjects preconditioned with concurrent stimuli performed better than subjects preconditioned with temporally spaced stimuli, as both of these groups had equal experience of the sound stimulus prior to the test phase. One is therefore disposed to believe in the genuine nature of the phenomenon.

As to the basis of the phenomenon, the absence of an effect due to prior exploration appears to show that an emotional (startle) response does not necessarily mediate preconditioning but the amount of prior exploration may have been insufficient or the interval between the last period of exploration and preconditioning may have been too long.

In summary: This experiment validates the status of preconditioning in two ways: (*a*) it indicates that Reid's criticism is unwarranted, which points to the possibility that his negative experimental finding may have been due to an insensitive procedure; (*b*) it shows that preconditioning is reduced by a temporal spacing of CS and UCS, and is therefore sensitive to a procedure which has been shown to effect classical conditioning.

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APPARATUS

A NEW COLOUR MIXER AND EPISCOTISTER

BY

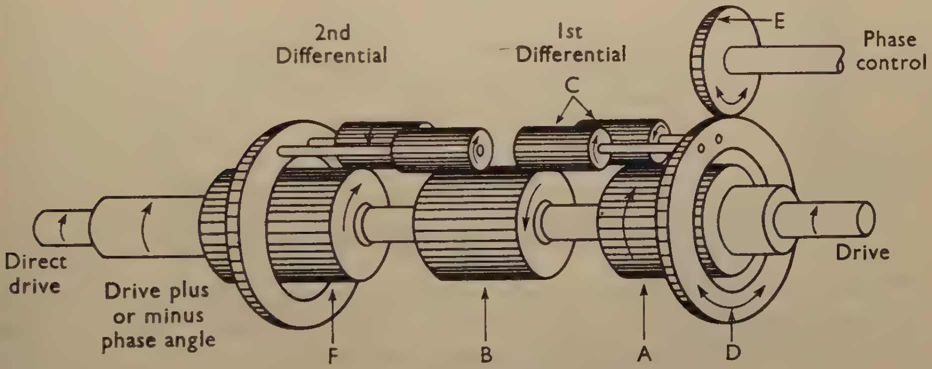
A. PERRY and I. P. HOWARD

From the Department of Psychology, University of Durham

The paper describes the construction of a differential system which can be used as a colour mixer or flicker apparatus. The use of sectored discs has been largely replaced by filters, wedges and polaroids in much visual work. However, our apparatus has two main applications, as a convenient, inexpensive colour mixer for student work and as a research tool in the study of flicker fusion and kindred phenomena.

Most psychology laboratories would find use for a colour mixer which gives a continuous change in the proportion of one colour disc to another while the colour wheel is running. Such a device with sectored discs is also useful as a convenient and precise method of controlling light intensity or as a visual flicker apparatus with a variable on–off ratio. Commercially manufactured differential colour mixers are expensive and bulky. A less precise, though cheap, design was described by Young (1923). The present design combines cheapness and compactness with precision and relative ease of manufacture.

FIGURE 1



The system is based on the differential gear. In such a system a gear on an input shaft (A)* drives a gear (B) in reverse through two intermediate gears (C) The axles of the intermediate gears are attached to a housing with gear teeth on its periphery (D). A rotation of the housing through a given angle imparts a phase shift of twice this angle between the input and output gears. The control to D is through a 2:1 reduction gear (E) which enables the correct phase angle to be indicated on a 360° dial. A spring friction-washer on the shaft of gear E prevents the phase from shifting of its own accord.

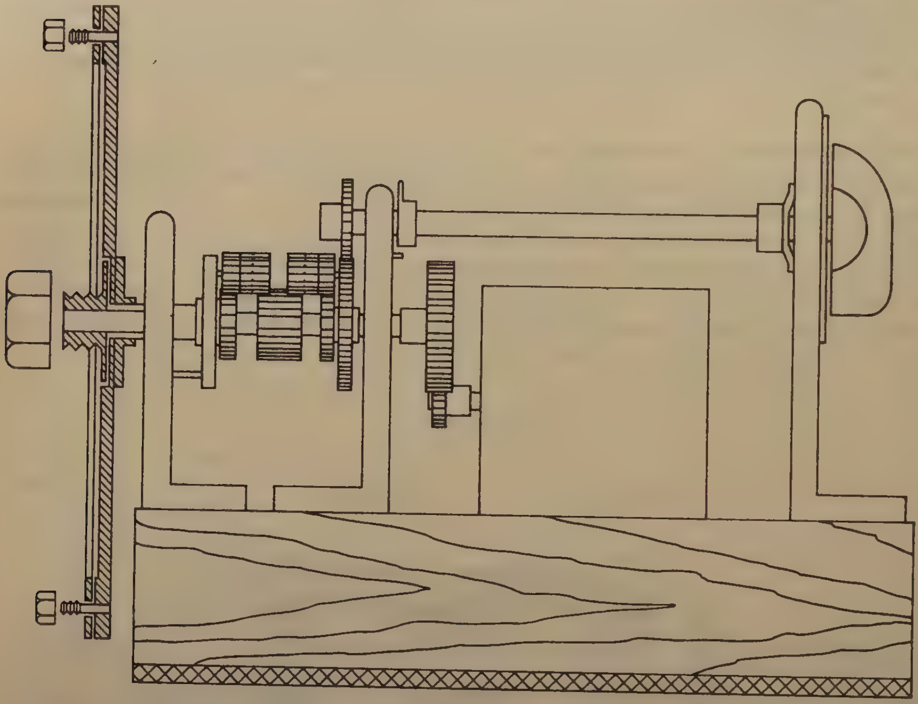
* The letters in the text refer to those on Figure 1.

The two shafts from a single differential rotate in opposite directions. The output gear from this first differential may be reversed by passing it into a second differential in line with the first.

The original drive shaft is brought through the hollow centre of the entire system to give two concentric shafts rotating in the same direction upon which may be amounted the coloured discs. The housing of the second differential (F) is held stationary.†

A gear coupling between motor and the input shaft is desirable to allow for any small misalignment and to give a step-down or step-up gear ratio if required. Small ball-race bearings make for smooth running.

FIGURE 2



The disc mounting is shown in section (Fig. 2) and allows about 350° phase shift; a small angle must be left so that the papers remain interleaved. The first colour disc is attached to the centre shaft emerging from the differentials by a half in. nut on a boss recessed into a $\frac{1}{8}$ in. thick plastic disc 6 in. in diameter. The second paper disc is attached to the plastic disc by a large plastic ring and thumb screw. The plastic disc is also recessed $\frac{1}{32}$ in. on its front face to the diameter of the first colour disc to allow the two paper discs to move freely relative to one another. The hole in the second paper disc and the outside edge of the first paper disc must be cut away slightly so that the discs avoid each other's points of attachment.

Sectored discs are easily attached for the mechanism to be used as a flicker apparatus rather than a colour wheel. A thick wooden base with sponge rubber on its underside gives stability and relative freedom from noise.

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† The differentials are obtainable from H. Franks, 58–60 New Oxford Street, W.C.1, Catalogue item No. 97, for a few shillings.

We have coupled two such systems together by a third single differential. With this we are able to stimulate each eye separately at the same frequency and vary the on–off ratio of flicker independently to each. At the same time the phase of the flicker to one eye may be varied relative to that of the other. This is very much cheaper and less bulky than the equivalent electronic circuitry. A very accurate frequency is maintained by driving the system with an oscillator controlled Desyn motor, $\frac{1}{2}$ in. in diameter. Using small differentials from old coin-slot meters, this flicker apparatus occupies the volume of a 4 in. cube.

Reference

Young, P. T. (1923). A differential colour mixer. *J. exp. Psychol.*, **6**, 323–43.

BOOK REVIEWS

Verbal Behavior. By B. F. Skinner. London: Methuen. 1959. Pp. x + 478. 42s.

Skinner tells us that this book had its origins in a challenge put to him by Whitehead in 1934. They became engaged in a prandial discussion about behaviourism. Whitehead agreed that "science might be successful in accounting for human behavior provided one made an exception of *verbal* behavior. Here, he insisted, something else must be at work. He brought the discussion to a close with a friendly challenge: 'Let me see you,' he said, 'account for my behavior as I sit here saying "No black scorpion is falling upon this table".' The next morning I drew up the outline of the present study."

How does Skinner meet the challenge? By giving us what he calls "a functional or causal analysis" of verbal behaviour. By the latter term he means, at the outset and provisionally, "behavior reinforced through the mediation of other persons." "The basic facts to be analysed," he tells us, "are well known to every educated person." By "functional analysis" he means in effect a description of these facts in terms of his own behaviour theory. "The emphasis [of the analysis]," he writes, "is upon an orderly arrangement of well-known facts, in accordance with a formulation of behavior derived from an experimental analysis of a more rigorous sort. The present extension to verbal behavior is an exercise in interpretation rather than a quantitative extrapolation of rigorous experimental results." He argues that the traditional formulations and concepts are of little help in attempting to arrive at a functional analysis. Thus he finds no use for concepts such as word, meaning, proposition, sign, symbol, intention of the speaker, and the like. Consequently, he has to devise new concepts of his own. The upshot is a long book containing a number of unfamiliar terms, in which the field of verbal behaviour is systematically described in Skinnerian language.

Let us pick out a few of the details in this grand exercise. Skinner begins by noting the chief features of verbal behaviour as a dependent variable. The unit that he selects is "an operant," but this cannot be identified by its form alone. For x to be an instance of a verbal operant, it must also be a function of some certain variable. The first type of verbal operant he distinguishes is "the Mand." This is one "in which the response is reinforced by a characteristic consequence and is therefore under the functional control of relevant conditions of deprivation or aversive stimulation." For example: "Listen!" "More soup!", "Pass the salt!" He then distinguishes three types of verbal operant that are under the control of verbal stimuli. These are: "Echoic Behaviour"; "Textual Behaviour" (for example, when a person is reading); and "Intraverbal Behaviour" (for example, when I say "Four" to the stimulus "Two plus two"). Next, he distinguishes "The Tact." This is "a verbal operant in which a response of given form is evoked (or at least strengthened) by a particular object or event or property of an object or event. We account for the strength by showing that in the presence of the object or event a response of that form is characteristically reinforced in a given verbal community." Here Skinner is obviously concerned with verbal behaviour in which we "talk about" the world. He goes on to describe "the Extended Tact" (in metaphor, for instance) and to deal with "Abstraction" and "the Problem of Reference." He discusses the role of the other important type of controlling stimulus that is also non-verbal, namely the audience; and he has a separate discussion of "the verbal operant as a unit of analysis," ending up this part of the book with a refinement of his definition of verbal behaviour. He continues in the next part by discussing some of the ways in which the controlling variables interact.

So far, however, he points out, he has assumed that the speaker does not know what he is saying, or wants to say, or how to say it. But "order, design and 'deliberate' composition are observable features of verbal behavior." Now these become possible, Skinner argues, because the speaker acquires a system of behaviour that controls his own behaviour; and Skinner uses this notion to introduce another new term, "the "Autoclitic." This term is "intended to suggest behavior which is based upon or depends upon other verbal behavior." He distinguishes various types of autoclitics. For example: (*a*) descriptive, where one "tacts" one's own verbal behaviour (for instance, "I believe . . .", "I surmise . . .", which describe the state of strength of a response; "I am happy to say . . ." indicates the emotional condition of the speaker; "I demand . . ."

tells the listener what kind of verbal operant it accompanies, namely a mand); (*b*) qualifying autoclitics (for instance, negation—"No," and assertion); (*c*) quantifying autoclitics (for instance, "a," "the"); and (*d*) those that are the traditional concern of grammar and syntax (such as inflections, the order in which responses appear, and predication). Skinner is at pains to try to show how the autoclitic activity of the speaker enables him to manipulate and control his own verbal behaviour, especially in composition. But, in addition to this, the speaker also examines his verbal responses for their effect on himself or listener, and they are then either rejected or released. Skinner calls this the "process of 'editing'." The last part of the book is taken up with a discussion of this process, and it ends with brief descriptions of logical and scientific verbal behaviour, and of thinking.

How, then, does Skinner answer Whitehead's challenge? The remark "No black scorpion is falling on this table" was meant to be a poser just because there was no black scorpion falling on the table—just because, that is, it was obviously *not* controlled by a present stimulus. But in a determined system there must have been some stimulus at work, even if it only weakly determined the form of the response. Now, just as a physicist at the present time may suggest various explanations of the fact that, say, there was a sudden drop in the temperature of the room at that dinner in 1934 (in order to show that the occurrence can be explained lawfully), so it is not out of place for him, Skinner, to make a guess today about Whitehead's remark. "I suggest, then," says Skinner, "that 'black scorpion' was a metaphorical response to the topic under discussion. The black scorpion was behaviorism." He continues a little further on: "It is possible, then, that as I described my position—doubtless in the most shocking terms I could command—he [Whitehead] was telling himself that the part which he had played in encouraging me as a young scholar was not entirely misguided, that I was probably not typical of all young men in psychology and the social sciences, that there *must* be a brighter side—in other words, that on this pleasant and stimulating table no black scorpion had fallen." Skinner adds that this explanation "is, of course, only a most improbable guess."

What are we to make of all this?

(1) To the outsider it is not immediately obvious how "the functional analysis" contained in this book will be of much help to the experimental psychologist—no matter whether the latter works inside or outside Skinnerology. If Skinner wanted the experimentalist to get something out of this book, he could have helped him by showing where the edifice can be brought down and tied to the earth of the laboratory. As it is, he scarcely mentions any experimental work, past or present.

(2) Is it logically necessary to spin this colossal story in order to answer Whitehead's challenge? No, it is not. Skinner himself makes this quite clear by his own answer: this is logically independent of his own functional analysis.

(3) Why, then, did he spin this story? He seems to have been trapped into supposing that Whitehead's question was one *inside* psychology, and not one *about* it. I think this supposition is a mistake. But given that he took the question as being one inside psychology, he naturally proceeded to answer it as a psychologist; and *in America* and *at that time* he could only be expected to answer it in one way, namely, by producing a large scale language which enables us to talk in a systematic way about the whole field of verbal behaviour. The book is to be understood, therefore, as a product of American culture—and perhaps, also, as a period piece.

(5) What is its value? Quite apart from any stimulus that the experimentalists may extract from it, it is of value in at least two different directions. It is an important exercise in theoretical psychology. Skinner has shown us what is involved in extending to verbal behaviour the apparatus of his behaviour theory. It is the first time, to my knowledge, that any leading theorist has attempted to talk in detail about linguistic functioning, and we should be grateful to him for his efforts. In making this attempt, he has brought closer together the two disciplines of psychology and logic. Here the book may be of help to many logicians and philosophers. It is time that the bogey of psychologism was slain, and a move made towards the construction of what Skinner calls "an empirical logic." He has probably given us some of the weapons necessary for this job; and students in this field will certainly derive a great deal from the insights and the analysis that this book contains.

B. A. Farrell.

The Bristol Social Adjustment Guides. By D. H. Stott and E. G. Sykes. London. University of London Press. 1958. Guides: Specimen Set 3s. 10d. Manual: *The Social Adjustment of Children.* Pp. 46. 25s.

The purpose of these "Guides" is the recognition of type and degree of emotional instability among children from 5 to 15 years of age. They cater for three different situations: the child in day-school, in residential care and in the family, the proformas being completed by school-masters and -mistresses, staff-members of residential centres and social workers, respectively. In each case, the Guide consists of four printed pages, giving brief, clear descriptions of different types of behaviour, classified under major headings.

For instance, the school guide includes items on Attitude to Teacher, to School Work, to other Children, Games and Play, Personal Ways and Physique. The guide for children in residential care covers some of the same topics but includes further questions on attitude to relatives, sleep habits, etc. The third proforma, the Family Guide, includes a life history chart and has sections on parent-child relationship, behaviour in home, health and development. The assessor is instructed to check one or more items that apply to the relevant child but to omit where no item is appropriate. He is asked to add supplementary comments where necessary. The items throughout are scrambled, in order to minimise halo effect; and most paragraphs include at least one "normal" response. On scoring the guide, a pattern emerges which gives some idea of the direction, complexity and extent of the child's divergence from normality—if divergence there be. These results are expressed in terms of, for example, Anxiety (X), towards adults (XA) or other children (XC); Depression (D); Withdrawal (W) or, less severe, Unforthcomingness (U); Hostility (H) or Hostility-Anxiety (HX); Knavery (K), which appears to be psychopathic anti-social behaviour; and so on.

Reliability is remarkably high for this field, correlations between pairs of teachers, for instance, being 0·78 for "unsettled scores" and 0·76 for "maladjusted scores." Validation has been achieved mainly inductively by comparing individual test-items and also "test-syndromes" with various predetermined groups, and repeatedly checking and improving the relationship. The authors do not, however, lose sight of the individual child in their appreciation of objectivity and of systematic research. They write, for example, that "the temptation to state the diagnosis in terms of a general quotient has been resisted. Any quotient or 'score' for maladjustment would be artificial because there are different ways of being maladjusted which are hardly comparable to one another." They withstand also the attractions of a typological approach, of statistics as an end in itself and of personality and trait psychology.

Inevitably, a number of criticisms suggest themselves. There is, for instance, too much philosophizing and self-interested history in the Section called "Methodology and Compilation"; there is, also, an infuriating tendency to assume familiarity on the part of the reader with the particular jargon chosen; and certain sections of the Manual suggest that, despite six years' work, publication in this form may be slightly premature. In general, however, the Guides are impressive. Stott and Sykes have tackled a perplexing problem without underestimating its difficulties and without oversimplifying method or interpretation. It is one of the most hopeful attempts yet made in this important field.

A. W. HEIM.

Figural After-effects. By Peter McEwen. (*British Journal of Psychology: Monograph Supplement,* No. 31.) London. Cambridge University Press. 1958. Pp. viii + 106. 22s. 6d.

A review of an experimental field, if it is adequate, may reasonably be expected to reveal deficiencies in experiment, to put controversial theoretical issues into sharper relief and so, directly or indirectly, lead to ideas for further experiment or to new theoretical questions. This monograph on figural after-effects meets these criteria in a satisfactory way.

Pride of place is given, rightly, to an account of J. J. Gibson's work as having been the first systematic description and investigation of visual phenomena of the kind which subsequently came to be called figural after-effects. But experimental work on after-effects, as the author states, has been dominated by the monumental series of effects described by Köhler and Wallach and, especially, by the satiation theory which they erected to account for them and to relate them to other visual phenomena. One third of the monograph is therefore devoted to a critical exposition of the work of Köhler and his collaborators in relation to later work. Included are their investigations of visual after-effects in the third dimension, of "kinaesthetic" effects analagous to displacements occurring in visual after-effects, and the attempt to give an account in terms of satiation of the destruction of illusions when repeatedly inspected. The examination is thorough and attention is directed to critical instances in which either observations reported appear at variance with expectation from the theory, or *ad hoc* extensions are made to the theory to account for them. The alternative "statistical" theory of Osgood and Heyer, to which another chapter is devoted, is treated similarly. What do perhaps emerge most clearly from this systematic exposition are the obstacles to rigorous deduction from either theory. Quantitative deductions, at least of relative magnitudes, are required. But the premises of both theories lack precision, argument from them has to be by circumlocution and an uncertainty of conclusion is the inevitable result. In the case of the statistical theory, the questions of the shape and scale of the distributions hypothesized are important if not vital. Neither question was considered in any detail by Osgood and Heyer. The basis of their theory in Marshall and Talbot's theory of visual acuity might with advantage therefore have been subjected to a more penetrating scrutiny. Deutsch's valuable, if negative, contribution on these points appeared when much of the monograph was written and the references to it are rather brief. Other data on acuity remain unconsidered, however, and their examination in relation to after-effects may yet prove fruitful.

A fourth chapter is devoted to other experimental studies. Included are reviews of work on kinaesthetic and auditory after-effects, as well as on visual effects in relation to apparent size, apparent movement and reversible figures. It concludes with the author's cautious appraisal of the present position. Generally, the monograph succeeds in giving a perspective to its topic. It does so even though some salient questions are touched upon, but not pursued. It provokes, rather than answers, such questions as the sense in which figural after-effects are distinguishable from other perceptual phenomena, how far the description "figural" is applicable to all of the after-effects so described, particularly as between sense modalities, and what might be their relation to other kinds of perceptual distortions and adjustments. That these, and other questions calling more immediately for further experiment, should be emergent, is nevertheless a measure of the value of this review.

ARTHUR SUMMERFIELD.

La Magie du Dessin. By Jean Vinchon. Bibliothèque neuro-psychiatrique de langue française. Bruges. Desclée de Brouwer. 1959. Pp. 182. 150 FRB.

Die Sprache der Zeichung. By Carlos J. Biedma and Pedro G. D'Alfonso. Bern. Huber. 1959. Pp. 110. Fr/DM 24.80.

Dr. Vinchon's book is a study of "doodling" and its supposed psychological significance. Although not experimental, it contains much interesting material, normal and abnormal, and a fairly level-headed commentary. Some discussion of the place of art in psychotherapy is attempted.

Dr. Biedma and Dr. D'Alfonso give an account of their new version of the Wartegg drawing test, which is supposed to have value in diagnostic personality study. They present a detailed analysis of the various features of style and expression elicited by the test, and claim some validity for their interpretations. The method may be of some interest to clinical psychologists of projective inclination.

O. L. ZANGWILL.

CORRIGENDUM

The ratio on p. 198 (line 3) and on p. 201 (line 8) of the article by A. T. Welford in the November, 1959 issue of this *Journal* should read 1/1.59 instead of 1.59/2.

PUBLICATIONS RECEIVED

NEW PERIODICALS

The following publications have been received:—

Activitas Nervosa Superior. Vol. I, Nos. 3 and 4, 1959. Chief Editor: M. Horváth. (Published by the Society for the Study of the Higher Nervous Activity, Section of the Czechoslovak Medical Society, J. E. Purkyně, Prague). Obtainable from Artia, Prague 2, Ve Smečkách 30. English Summaries.

Grundlagenstudien aus Kybernetik und Geisteswissenschaft. Vol. 1, No. 1, January, 1960. Edited by M. Bense, F. von Cube, G. Eichhorn, H. Frank, A. A. Moles and E. Walther. (Technische Hochschule, Huberstrasse 16, Stuttgart.)

Izobrazba Rukovodilaca. No. 2, June, 1958. (Zagreb, TRG Žrtava Fašizma 4.) Industrial Psychology and Management Studies. English summaries.

Journal of Primatology: Primates. Vol. 1, No. 2, 1958. Edited by K. Andô, D. Miyadi, Y. Tajima and K. Imanishi. (Published by the Japan Monkey Centre, Kurisu Inuyama City, Aichi, Japan.) Japanese and English text.

Rehabilitation. (Section XIX of *Excerpta Medica.*) Vol. 1, No. 1, July, 1958. Edited by M. Fishbein, M. W. Woerdeman, and H. Ogilvie. (111, Kalverstraat, Amsterdam.)

OTHER PERIODICALS RECEIVED

Periodicals mentioned in the list published in this *Journal,* 1958, **10**, 176, are not included.

Archives Italiennes de Biologie. Vol. 97, No. 1, 1959. Edited by G. Moruzzi. (Pisa Universita Degli Studi, Physiological Institute of the University of Pisa, Via S. Zeno No. 11–13, Pisa.)

Japanese Journal of Psychology. Vol. 30, No. 4, 1959. Edited by M. Sagara and Y. Togawa. (Published bimonthly by the Japanese Psychological Association, c/o Faculty of Letters, University of Tokyo, Tokyo.) Japanese text with some English summaries.

Japanese Psychological Research. No. 8, 1959. Edited by T. Obonai and M. Sagara. (Published by the Japanese Psychological Association, c/o Faculty of Letters, University of Tokyo, Tokyo.) English text.

Psychologia Wychowawcza Kwartnalnik (Educational Psychology). Edited by M. Zabrowska. (Warsaw, ul. Spasowsklego Nr 6/8.)

Psychologie Française. Vol. 4, No. 3, 1959. Revue trimestrielle de la Société Française de Psychologie. Directed by P. Fraisse. (Société Française de Psychologie, 46 Rue St. Jacques, Paris 5e.)

Soviet Information Bulletins: Psychology. Vol. 6, Nos. 1 and 2, 1959. Price 3s. (Society for Cultural Relations with the U.S.S.R., 14 Kensington Square, London, W.1.)

OTHER PUBLICATIONS RECEIVED

Charles Darwin. By Sir Gavin de Beer. Henriette Hertz Trust Lecture of the British Academy, 1958. Oxford University Press, 1958. Price 3s. 6d.

Manual of the Maudsley Personality Inventory. By H. J. Eysenck. University of London Press, 1959. Price 2s. 6d. net.

Tobacco Manufacturers' Standing Committee: Research Papers No. 2. The Reliability of Statements about Smoking Habits. By G. F. Todd and J. T. Laws. (6–10, Bruton Street, London, W.1.)

PERGAMON INSTITUTE

The Pergamon Institute (English address: Headington Hill Hall, Oxford) announce that English editions of the following journals are being prepared: *Pavlov Journal of the Higher Nervous Activity*, *Problems of Psychology* (selected papers) and *Problems of Cybernetics.* Specimen copies and subscription rates on application. A series of monographs in translation, including some psychological titles, is also in preparation.

ZEITSCHRIFT FÜR EXPERIMENTELLE UND ANGEWANDTE PSYCHOLOGIE

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Band VI/4

ADOLF OTTO JÄGER, Einige emotionale, conative und zeitliche Bedingungen des Erinnerns.

FRIEDRICH CZAGAN, Die Verwendung lautlicher Ausdrucksmittel zur Wiedergabe von Körpereigenschaften.

ELISABETH PAVLIS, Aufmerksamkeitsschwankungen in kurzen Reaktionszeiten.

HANS HÖRMANN, Untersuchungen zur sog. "Manifesten Angst."

GUSTAV A. LIENERT und ROBERT LIENHÖFT, Versuch einer Standardisierung der Drahtbiegeprobe.

GERHARD HERRIG, Rigidität bei ländlichen Jugendlichen.

EMIL SCHMALOHR, Die Auswirkungen des ganzheitlichen und lautsynthetischen Schreibleseunterrichts auf den späteren Schulerfolg.

WALTER TRÖGER, Die kritische Phase der 16_ und 17jährigen. Kritische Buchbesprechung.

W. MEYER-EPPLER, Grundlagen und Anwendungen der Informationstheorie. Kummunikation und Kybernetik in Einzeldarstellungen.

All articles are provided with summaries in English and French.

The journal appears quarterly and contains 160 pages per number.

Subscription is DM 64.—per volume.

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THE QUARTERLY JOURNAL OF EXPERIMENTAL PSYCHOLOGY

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